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POSTGLACIAL CLIMATE IN EASTERN NORTH AMERICA *†

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The character of past climates is inferred from a variety of facts, all fragmentary and often misleading. Giles (7), for example, has recently shown how uncertain is the evidence commonly used to prove that the climate of the Coal Age was a tropical one.

Yet we are reasonably sure of great climatic changes in the past. Three major periods of glaciation—Pre-Cambrian, Permian and Pleistocene—have left their traces. Their total duration appears to have been much less than that of the intervening milder climates—climates whose mildness may be gauged by the occurrence of coal beds within 9° of the north pole and well into the now barren antarctic.

Brooks (3) and others consider our present climate closer to the glacial than to the more prolonged mild climates. In this sense the present is not the normal terrestrial climate and might be expected to exhibit some instability as a result. In point of fact there is good reason to believe that there have been marked fluctuations of both temperature and moisture since the last, or Wisconsin, glaciation. These climatic changes of Quaternary time seem to have been more than a simple steady warming as the ice-sheets receded.

A great deal of evidence regarding postglacial climate has been secured in Europe. It is of many sorts but in general appears to support the so-called Blytt-Sernander hypothesis (16). The essential feature of this theory is that there have been two periods of great dryness—*i.e.* of continental climate—in Quaternary time. These have alternated with periods of greater humidity—*i.e.* oceanic climate—the present being an example. The assumptions regarding temperature are not so clear-cut, the dry periods being generally considered warm while the moist ones are differently designated by different investigators.

If one consider the complexity of climate and the diversity of a continent like Europe it is remarkable that even a rough agreement has been reached.

* Contribution Botanical Laboratory, University of Oklahoma, No. 9.

† Expanded from a paper read at the Symposium on "Glacial Relicts" before the Systematic Section of the Botanical Society of America, Cleveland, December 1930.

The terms "warm," "moist," etc., are in themselves no standards on which to base a safe generalization. Thornthwaite (15) in this country has recently developed a set of mathematical indices which appear to promise a sounder integration of temperature and moisture in relation to biological areas than any we have had. It is to be hoped that these, or some better means of designating climates in America will be used before too sweeping generalizations are drawn, and particularly before names are given to hypothetical climatic periods.

The length of postglacial time in North America is variously estimated, but most estimates agree upon the order of magnitude. Figures between 30,000 and 40,000 years are usually accepted. Antevs (1) and others have been counting the varves or annual deposits of clay in New England and Canada in an effort to secure a precise time table. They have accurate data for limited periods, but these periods do not as yet appear to be connected together or with the present.

The rate of growth of peat deposits is not sufficiently understood to be a safe guide. Here again there is some agreement on the order of magnitude, but that is all. Dachnowski (4) mentions two centuries to the foot, Soper and Osbon (14) the much lower figure of 1-2 inches per century. My own preliminary estimates based on observations of frozen sections suggest a rate of about 25 years to the inch in Ohio and Michigan for average consolidated peat. This is a line of investigation which should be pushed.

Dachnowski (5) considers that climatic variations are among the causes of differences in peats studied by him, but recognizes the difficulty of discriminating between local and climatic influences without microscopic study.

A most helpful work on postglacial climate in eastern North America has been that of Gleason (9), based mainly on floristics. Extending the earlier idea that bogs are relicts of the subglacial tundra, he recognizes the presence of numerous relicts of western vegetation as well, in the north central states. Prairies in the present deciduous forest region are the best examples of this. From such evidence he infers that postglacial time has been marked by a prolonged warm dry period. He also has data to show that recently the forest has been invading the prairie—suggesting an increase in humidity.

In Ohio the writer has charted the position of numerous socalled relicts of both tundra and grassland vegetation and indicated that the native forest there has been increasing in mesophytic character and number of species (13). This seemed to confirm Gleason's theory, except possibly in the matter of temperature. The fact that bogs had survived the postglacial dry period suggested that this had not been excessively warm, but rather like the grassland climate of Manitoba. This latter conclusion was based, however, upon a too static conception of the character of relicts.

Since these papers have appeared peats in at least four regions of North America have been subjected to microscopic analysis. The purpose of this analysis is to determine the proportions of pollen of different sorts blown in

from adjacent vegetation at successive times. From this some notion of the vegetation and so, perhaps, of the controlling climate is obtained.

Lewis and Cocke (10), reporting on samples from the Dismal Swamp of Virginia, have calculated proportions on the basis of all spores found. They get evidence that forest development was twice checked as this swamp progressed from an open to a closed one, but have been very cautious about drawing climatic inferences. Recalculating their figures to eliminate fungus, moss, and fern spores gives interesting results. Two clearly marked pine-hickory maxima appear, with a strong grass maximum between. Whether the grass is a climatic phenomenon, or due to extensive submergence is not clear, but pine and hickory plainly suggest a somewhat dry or sub-continental climate. Moreover, this entire interval (from 10 to 3 feet) corresponds in position and extent to the more recent of the two dry postglacial periods elsewhere postulated in Ohio and Canada. Further work in the Dismal Swamp region should be awaited with great interest. It is to be hoped that diatoms as well as pollen may be studied to elucidate changes in water character.

Auer (2) has published graphs of the fossil pollen in 23 bogs in southeastern Canada, but limitations of space have prevented publication of his detailed notes. In general these graphs show that the deposits began in a period of pine and spruce. Above this is a hemlock maximum, then Carex peat with deciduous forest, and raw sphagnum peat on top. This means, according to Auer, two periods of continental climate, the second warmer than the first. Alternating with them have been two periods of humid climate, of which the present is one.

Meanwhile the writer has been investigating a number of peat deposits lying within a two hundred mile square area, extending from Indianapolis, Indiana east to Wooster, Ohio, and from Ann Arbor, Michigan south to Lancaster, Ohio. This comprises a substantial section along the moraine fronts. It is moreover so located between oceanic and continental extremes that any fluctuations of moisture might be expected to show clearly, provided they were of sufficient magnitude and duration to affect vegetation on a considerable scale. In addition, material from Iowa has been under investigation, as will be noted.

Samples from over twenty bogs have been secured and in all cases examined show that deposits of coniferous pollen underlie those of deciduous pollen. The first published account of any of these bogs was a brief preliminary note by Miss Draper (6). This deals only with the upper deposits of the New Haven bog, and has since been rechecked from additional material. Both the original and revised report agree in indicating that tree pollen is relatively much more abundant near the surface than at depths below two feet. Grasses and composites are conspicuous below this level, suggesting more prairie-like conditions than at present.

The next account (11) deals with the Bucyrus peat deposit. This section

of fourteen feet shows a clear cut transition from fir-spruce through spruce-pine to pine, suggesting progressive desiccation during a cool coniferous period. A hiatus or water pocket occurs in the second foot and above this pine is quickly replaced by deciduous tree pollen. Although some erosion, fire, and oxidation through exposure were known to have affected the upper surface, the extent of this destruction of the deciduous forest record was not appreciated until numerous other bogs had been examined, and the Mud Lake Bog (12) studied in detail. This latter deposit afforded a column of 25 feet, 24 of which consist of deciduous forest deposits, largely. Below this appears the coniferous forest record, condensed because of slow marl and silt deposition during the early history of the lake, which lies in a much deeper basin than the Bucyrus deposit.

In Mud Lake the record begins with fir-spruce as it does in the Bucyrus deposit. Progressive desiccation during coniferous times is suggested again by the fact that oak-hickory-pine pollen marks the transition to deciduous deposits. Above this level there is a definite increase of beech at the expense of oak and hickory then a prolonged reversal of this condition, with oak and hickory dominant. In the uppermost layers a second reversal is indicated with a corresponding decrease in hickory, especially.

If any conjecture may be based on such results it is that deciduous time has had largely a somewhat continental climate, drier at any rate than the present and separated from the dry late coniferous climate by a period favorable to the growth of beech.

Lane's (9) studies of the McCulloch bog in Iowa strengthen our evidence for postglacial desiccation. He shows coniferous forest replaced by deciduous, then prairie twice interrupted by waves of amaranth-chenopod vegetation—essentially semi-arid. The exact relation of these two periods of apparently semi-arid climate to the changes in Ohio cannot be settled until further work is done.

In Table I a correlation of these various results is presented, with full realization of their tentative character. If Auer is correct, and our interpretation of the combined Bucyrus-Mud Lake columns not at fault the parallel between climatic changes in Europe and America is a striking one. Yet much more work is needed before any *ex-cathedra* pronouncements are made.

Meanwhile, no matter what details must be revised it seems more than a coincidence that all of the work reported indicates a recent decrease of those types of pollen fossils suggesting desiccation. This must be looked on as an independent line of evidence strengthening the inferences drawn by Gleason on floristic grounds.

If these inferences are sound the vegetation pattern of the north central states becomes intelligible. The patchwork of plant communities—beech-maple—mixed mesophytic—oak-hickory—prairie relicts—tundra relicts, correlated in broad outlines with topography (13) are the inevitable ex-

TABLE I. *Suggested correlation of pollen deposits in Eastern North America*

	S.E. Canada (Auer)	Virginia (Lewis & Cocke)	Ohio (Sears, Draper)	Iowa (Lane)
I. Humid.....	Spruce and raw peat; cool?	Mixed gum forest, warm	Mixed deciduous, warm	Grassland, warm
II. Dry.....	Deciduous forest and sedge meadow, warm	*{Pine-grass Hickory maxima Warm	Oak hickory prairie, warm	Arid grass-land, warm
III. Humid.....	Hemlock, cool	Marsh?	Beech and mixed deciduous moderate	* Grassland, warm
IV. Dry.....	Spruce and pine, cool		Pine, cool	Arid grass-land, warm
V.....			Spruce-pine, cool	Deciduous forest, moderate
VI. Humid.....			Fir-spruce, cool	Conifers, cool

* Both clearly xeric; duration of either uncertain; correlation here based upon assumption that peat accumulated more slowly in Iowa than Virginia.

pression of slowly shifting climates. And the relation to major physiographic features must be sought, in a measure at least, in the effects of such features in hastening or retarding the expression of climatic shifts in terms of plant communities.

Acknowledgments are due the National Research Council and the Department of Botany, University of Michigan.

SUMMARY

The preceding paper presents a tentative correlation of available data on the stratigraphic distribution of fossil pollen in peat deposits of eastern North America. The results suggest a strong parallel with European post-glacial fluctuations, and indicate two major periods of desiccation, or continental climate, the second warmer than the first. The reality of one such period would be sufficient to lend weight to Gleason's conclusions as to post-glacial climate, based on floristic studies, and to greatly clarify the present vegetation pattern of the Great Lakes area.

The provisional character of all reconstructions of past climate has been borne in mind throughout, and the need for continued work emphasized.

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RHYTHMIC PERIODICITY AND SYNCHRONOUS FLASHING IN THE FIREFLY, *PHOTINUS PYRALIS*, WITH NOTES ON *PHOTURUS PENNSYLVANICUS* *

PHIL RAU

Kirkwood, Missouri

Fireflies have charmed us, always. They come out of the cool grass in the hush of twilight, and their silent, rhythmic glow as they glide into the deepening shadows lulls us to rest and childish fancy, rather than stimulates us to an alert inquiry as to what it is all about.

In recent years some attention has been given to the two phases of their activity suggested in the above title. Prominent among these is a paper by Mast¹ who shows, among other things, the relation between luminosity and the sexual function of the firefly, *Photinus pyralis*. Here appear the following statements, which have a direct bearing on the rhythmic periodicity of the activities of these insects (p. 259). "The time of the day when the first glow appeared was surprisingly constant throughout the season." "I have no evidence indicating that the fireflies, as might be expected, appear earlier on dark, cloudy and rainy days than on bright, clear days." Specimens kept in darkness or in low light intensity during the day did not become active earlier than those under normal conditions, and finally, "Thus it appears that the activity of these creatures is a periodic phenomenon to a considerable extent independent of environmental changes."

In a recent work on the sex life of the saturniid moths,² I ascertained that while in nature each moth became active once in each period of twenty-four hours, this activity was brought about by certain intensities of light; if these light conditions were simulated at other times of day, the moths would respond as often as the optimum light appeared.

I suspected that, contrary to Mast's statement that this phenomenon is independent of environmental conditions, the periodic activities of fireflies would likewise be influenced by conditions of light, i.e., that when the light reached a certain intensity, the fireflies would become active. Every summer these insects are plentiful about my two and one-half acre tract, so I decided to make close observations on their spontaneous action in this open space.

Photinus pyralis was first observed on May 15, in 1929, but may have

* Specimens identified by Mr. H. S. Barber.

¹ Mast. Behavior of fireflies, with special reference to the problem of orientation. *Journ. An. Beh.*, 2: 256-272. 1912.

² Rau, P. and N. The Sex attraction and rhythmic periodicity in giant saturniid moths. *Trans. Acad. Sci. St. Louis*, 26: 81-221. 1929.

been out in limited numbers several days before that. In 1930, a close watch was kept for the first flash of the season; this occurred on April 28. Occasionally a few were seen thereafter, but they first appeared in fair abundance on May 5. The technique for examining the problem under absolutely natural conditions was simplified when I noticed that sometimes they flashed in the dense woods when they did not out on my open lawn.

Fortunately, this convenient tract contained a variety of exposures to light. The front or southern half of this lot has the house in its center, with an open lawn edged by shrubs on either side. Some distance back of the house is a tiny but very dense grove covering about one-half acre, and beyond that an open weed-patch, fully exposed to the slanting rays of the afternoon sun. Naturally, at twilight the edge of the woods and the shrubbery at the edge of the lawn would offer a diffused light midway between that of the deep thicket and the open lawn. Hence the following light-areas were recognized: open lawn, dense woods, edge of the woods, and weed-patch. Of course the lawn and the weed patch were somewhat similar, but since one was covered with weeds and the other only with short grass, and the woods separated them, they were considered separately. I did not begin the study until all four areas had displayed an abundance of fireflies, on July 4.

Of the two species the black beetle, *Photinus pyralis* flies early in the evening, and *Photurus pennsylvanicus*, the brown one, flies later, when it is fully dark. The first performs its flight, keeping low over the vegetation; after 8:45, they become fewer, and by 9 o'clock, one of them can seldom be found on the wing. At that time the brown ones, *Photurus pennsylvanicus*, take their turn at brightening the fields. These wend their way upward, and are soon floating away over the tree-tops. They continue their flight practically all night; I have seen the latter in flight as late as 2:30 A.M., but not at 4 A.M. on several examinations. Throughout the season's observations, these facts remained unvaried: one species occupied the stage during the twilight hours, in low flight, and as soon as real darkness arrived, they surrendered the place to the other species, which flew high and until near the approach of dawn. Several of each species which were kept in a large glass box in the yard for closer observation behaved in just the same way.

On July 4, in order to be more systematic, I stationed members of my family at the four stations enumerated above, to sound the alarm of the first appearance of the fireflies at each place.

In another glass box in the laboratory, where the daylight first faded, the black fireflies of both sexes first became active. At 6:48 they moved and flew about as much as the box would permit, flashing abundantly. Some twenty were in the box, and most of them were in motion. Ten minutes before, they had all been as quiet as they had been at midday. At this time the watchers on the other locations reported no beginning of activity. At 7:02, the first one appeared in the dense woods, and within the next

minute or two several more became active. Those imprisoned in the glass box in the shade of a tree in the yard began to flash at 7:05. Not until 7:15 did two individuals illuminate the edge of the dense grove, and within three minutes many others came forth from the shrubbery to join them. The unshaded areas were still without any flashing blettes. These two areas, the open lawn and the weed-patch, although not adjacent, gave forth their flashing fireflies almost simultaneously at 7:26 P.M. Only a few began the display in each area, but others appeared at so nearly the same time that within three minutes, hundreds were twinkling over the lawn and weed-tops.

Theoretically, if rhythmic periodicity determines their activity, each day when the clock points to a certain minute, all these insects should become active, regardless of their location. If, on the other hand, light of a certain intensity rouses them to action as the above experiment indicates, it can not be termed rhythmic periodicity, but a responsive reaction to light.

These crude experiments show how delicate is the gradation of the light intensity to which they respond. The light is not the same at any one time, say 7:15, in shaded forest, edge of the forest and open lawn, but it is similar enough that organs of sense must be very delicate to make the fine discrimination so accurately.

Two weeks later, I decided to repeat the observations, because Mast is very decided in his opinion that the insects are not influenced by condition of light. The methods were the same: the four distinct areas were watched as before.

They began to flash in the dense woods. At 6:44 the first one was seen, within a minute six more were seen. In the other regions none were yet visible. By 6:49, dozens twinkled in the woods.

At 7:08, several appeared almost simultaneously at the edge of the woods and in the shrubbery at the edge of the lawn. The open lawn did not share in the festival of light until 7:15, and not until 7:30 did they appear in numbers over the treeless weed-patch, the spot last touched by the rays of the afternoon sun.

Similar observations in part or all of the areas on six other evenings yielded practically the same results. If the evening was cloudy, they would begin slightly earlier.

On June 25, the sun shone until mid-afternoon, when a black storm-cloud suddenly darkened the sky. It became so dark that the chickens were seeking an untimely roost, as they do during an eclipse of the sun. In the dim hush before the onrush of the storm, the twilight picture was made complete by the appearance of six fireflies, rising from the flowerbeds in the yard, and flashing as though all were normal.

That the brown firefly, too, has its activities influenced by conditions of light was seen in an incident on June 15, 1930. When clouds suddenly caused it to become pitch dark from 8:12 to 8:18 P.M., hundreds of *P. pennsylvanicus* burst into action and were flashing beautifully for those six

minutes. These normally do not appear until 9 o'clock, after the last gray of twilight has faded. This period of abnormal darkness did not completely stop the flight of the black fireflies which were already in action: most of them continued until almost 8:45, their normal time for subsiding. Thus *P. pennsylvanicus* reacts to a certain degree of profound darkness as *P. pyralis* does to a certain degree of twilight.

These simple observations reveal two interesting points: (a) There is a difference of 25 to 40 minutes between the time of their appearance in the woods and in the well-lighted spaces, although the different areas are at no point more than three hundred feet apart. (b) As the summer advances, they appear slightly earlier, in the great majority of cases. This earliness agrees surprisingly well with the difference in the time of sunset after the summer solstice. For instance, they appear from eight to eighteen minutes earlier in their respective areas when the sun sets thirteen minutes earlier. These consistent adaptations to the variations of the light, in addition to the instance of their responding to dim light under unusual conditions at midday, lead me to conclude that these creatures are stimulated to action by definite light conditions, and not by a blind, rhythmic impulse from within. There is always danger of the simple error of mistaking rhythm in the stimulus for rhythm in the creature.

And now a word concerning the problems of rhythmic periodicity which are now being recognized by naturalists to a far greater extent than ever before. It sometimes happens that no distinction is made between actual rhythmic phenomena which occur within the organism, and the regularly recurring action which is influenced by environmental conditions. I believe the fairly regular action of the two species of fireflies to be of the latter sort. If the fireflies would become active once in each cycle of twenty-four hours (or any other length of time) at a stated time, regardless of its surrounding lights or shadows, the cause of the action could rightly be called rhythmic periodicity. I am inclined to say that those actions which require a stimulus to start them, [as a certain intensity of light does in this case] are only reactions, or adaptations in behavior, while those actions which require outside influences to stop them or modify them [e.g., the heart-beat] may truly be termed rhythms.

Another phase of the activity of the fireflies which has elicited much controversy is the question of their synchronous flashing. It has been said, and again denied, that the population of a region shows a marked tendency to flash rhythmically in unison.

For years I have watched to discover a clear case of this phenomenon, which other observers profess to have seen, and at last, in one and only one instance, did I witness a case of synchronous flashing. At dusk on June 4, 1922, a companion and I saw this beautiful spectacle. Publication of this note was delayed, in the hope that some time again I might find an instance, and discover some clue to the cause. Since in the years of watching, all

later observations have shown only the opposite behavior, I can only conclude that some peculiar condition of environment or weather was responsible for the marked case which I witnessed.

We were walking along the railroad track near Kimmswick, Missouri. The track is at the foot of a bluff which skirts the Mississippi River bottom, and from its elevation we could look down upon the dense vegetation between the railroad and the river. Twilight was deepening; a light summer shower had just ceased. Suddenly hundreds of fireflies seemed to rise and glow simultaneously over the broad, low field. Their unified flashing was unmistakeable, and we watched it, charmed by the beauty and wonder of the scene, for a few minutes. After perhaps four or five minutes, however, the rhythm was lost in chaos, as usual, and was not resumed.

The only explanation that my imagination offers me for this case is that perhaps the entire population was ready to rise in flight but was held back by the shower; when this suddenly ceased, they were all in equal readiness, and at the propitious moment took to wing and flashed together. Since their flashes are at a fairly uniform interval, they continued in unison, quite by accident, and did not break step for a few minutes.

This note would hardly be worth publishing except for the fact that in the literature much controversy exists as to whether or not synchronous flashing occurs. This instance convinces me that it does occur, but very rarely, and under certain limited conditions. Perhaps the explanation lies in the surrounding conditions, such as the moist, heavy air, the sudden cessation of the shower, the lack of breeze, and perhaps other ingredients that make a combination suitable for this phenomenon.

LIFE FORMS AND LEAF SIZE CLASSES OF CERTAIN PLANT COMMUNITIES OF THE CINCINNATI REGION

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Introduction

The influence of the climatic factors, temperature and rainfall, on plant formations, species distribution and vegetative structures is pronounced. The effect of edaphic and physiographic features is just as striking on a somewhat lesser scale. Rainfall and temperature determine the major formations as desert, grassland and forest. Edaphic and topographic characteristics produce local variations within these formations. Exposure, run-off and soil type may be conducive to the persistence of associations within major plant communities which are totally unlike the climatic climax or its seres.

The several groups within a given climatic region, as the climatic climax, the physiographic climates, and relict colonies, exhibit a lack of similarity in matters other than species composition. The physiognomy and general gross physical structure differ in a greater or lesser degree from association type to association type. The work discussed in this paper is an effort to deal in a detailed statistical manner with these differences by means of leaf size and life form classifications of the plants of such diverse communities within the Cincinnati region. The methods of Raunkiaer (4, 7) are used as a basis, with certain slight modifications which have been made to render his classifications more suitable.

General Features of the Cincinnati Region and Certain of its Communities

The Cincinnati region is near the southernmost extremity reached by glaciation in North America. The soil is Illinoian till on the uplands and on some slopes; Wisconsin outwash gravels form terraces in certain valleys while residual limestone soils prevail in most ravines. A deep alluvium fills the larger valleys.

The rainfall averages 38.63 inches per year¹ (fig. 1) (1) and the temperature averages 53.2 F.² (fig. 2). The average growing season is 194 days, the average date for the last kill-frost in the spring being April 14 and for the first one in the fall, October 25. Killing frosts have been known as late as April 26 and as early as September 30.

¹ Average from record of last 20 years or more.

² Average from record of last 30 years or more.

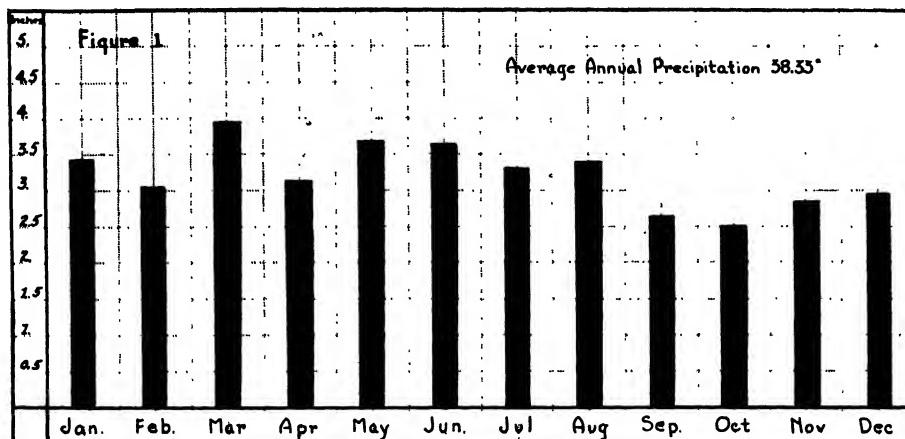


FIG. 1. Average monthly precipitation of the Cincinnati region.

The associations to be compared and contrasted as to leaf size and life form consist of five community types, four roughly representing the three great climatic formations of forest, desert and grassland, the fifth representing the hydrophytic type.

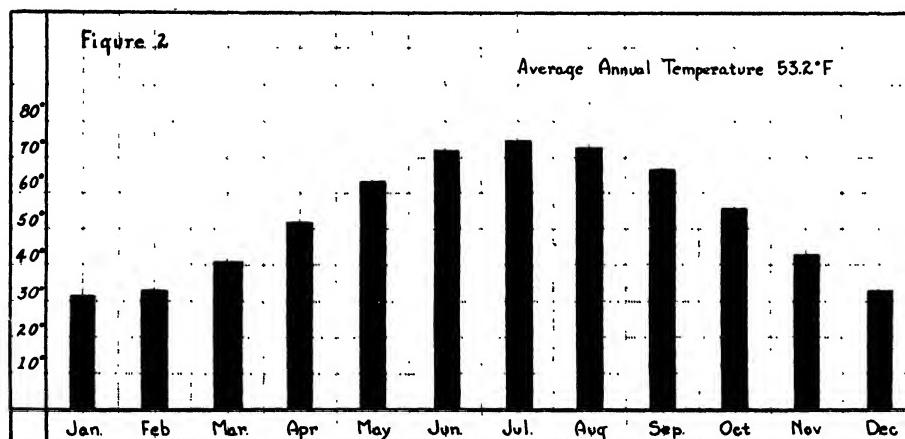


FIG. 2. Average monthly temperature of the Cincinnati region.

CLIMAX MIXED MESOPHYTIC DECIDUOUS FOREST

The climax vegetation is a mixed mesophytic deciduous forest (fig. 3) with *Fagus grandifolia*,³ *Acer saccharum*, *Liriodendron tulipifera*, *Aesculus octandra*, and *Fraxinus americana* as dominants. The undergrowth is dense and varied with an especially rich herbaceous flora. The climax is found in areas of intermediate edaphic conditions, especially on the numer-

³ Nomenclature from Gray's New Manual of Botany, 7th ed.

ous gentle slopes and in the protected ravines (1). It is the climatic vegetation and may be thought of as the type best in accord with the temperature and rainfall of the region.



FIG. 3. Mesophytic climax forest.

UPLAND FOREST

A second forest type present in the region is the pre-erosion climax and its successional stages. The pre-erosion climax is dominated by beech and is not common near Cincinnati, its range being somewhat to the east. The climax itself does not offer such interesting vegetational possibilities as some of its successional stages, especially the pin oak association with its forest openings which is especially well defined and fairly prevalent. The pin oak stage offers a striking contrast to the true climatic climax of the region

and for this reason was selected rather than the pre-erosion climax beech forest.

The pre-erosion successional series is found on the flat, undrained, acid uplands which present a younger physiographic condition than the eroded slopes and ravines.

As to physiognomy, the pin oak forest and its openings contain a number of shrubs with a comparatively small number of herbs. Among the shrubs are found *Ilex verticillata*, *Pyrus melanocarpa*, *Viburnum dentatum*, *Spiraea tomentosa*, and *Vitis labrusca*. In the herbaceous ground cover are *Viola*



FIG. 4. Upland forest of pin oak type.

cucullata and *Aster umbellatus* with a number of sedges and a predominance of *Cardamine bulbosa* in spring. These plants, together with the mats of Sphagnum, are evidence of the acidity and saturated state of the soil.

GRASSLAND

A prairie colony at Miamiville (fig. 5) is the only true grassland area in the entire region. It is situated along the northern bank of the Little Miami River occurring on the bluff about thirty feet above the river level, surrounded on all sides by forested areas. The bluff has a south-south-western exposure and is steep, being subject to extreme slumping. The vegetation is exposed to drying west winds and intense heat. The soil is an alkaline clay (Illinoian drift), more or less impervious to water which runs

off the steep soil surface more rapidly than it can percolate through the soil pores, there being no spongy humus covering. However, the conditions are in nowise xeric.

The prairie has but one distinct association, that dominated by *Andropogon scoparius*, *Sorghastrum nutans* and *Silphium terebinthinaceum*. The vegetation presents a grassland aspect with a few small trees such as *Quercus rubra*, *Q. muhlenbergii*, and *Robinia pseudo-acacia*, all of which are in poor condition. Although of small stature, many of these trees have rounded out a good half century of life.



FIG. 5. Prairie opening near Miamiville, Ohio.

The presence of this relict group has been directly correlated with the post-Wisconsin xerothermic period when an eastern lobe of the grassland probably extended across the Cincinnati region. As the xerothermic period passed and the climate became more humid, the mesophytic forest successfully invaded the prairie until at the present time, the grassland persists only in such areas as are edaphically unfavorable to forest. Irwin (5) has discussed the Miamiville colony.

XEROPHYTIC COMMUNITY

The third type of situation selected is located on the site of an abandoned gravel pit (fig. 6). The most extensive portion occupies a flat area of almost direct southern exposure along a twenty-five to thirty-five foot vertical cut.

The soil is composed largely of sand and gravel (Wisconsin outwash) with a very thin humus covering in some places. In the same vicinity are several sandy flats with conditions which approach the xeric being brought about by an excessive exposure to sun and wind in combination with a minimum amount of available moisture.

Such species as *Croton monanthogynus*, *Isanthus brachiatus*, *Polanisia graveolens* and *Opuntia spp.* are among the common floral constituents. This community is relatively unstable and not certainly defined as an association.



FIG. 6. Xerophytic community at Terrace Park, Ohio.

HYDROPHYTIC COMMUNITY

Pond and swamp habitats are not found to any great extent in the region except on flood plains. Most of the natural areas have been drained and only a few small ones together with a number of artificial depressions remain. *Nelumbo lutea*, *Typha latifolia*, *Alisma plantago-aquatica*, *Polygonum muhlenbergii*, *Sparganium eurycarpum* and *Leersia oryzoides* are among the predominant hydrophytes with *Salix nigra* and *Populus deltoides* common along the pond banks. Included as the hydrophytic association species in the life form and leaf size classifications are those plants occurring in the pond proper, those along its direct margin and the plants which occupy the area either flooded or saturated by the pond water.



FIG. 7. Hydrophytic community at Addyston, Ohio.

Geographical Affinities of the Communities

In order to emphasize the relation of the above five communities to their geographical affinities, the distribution in the United States of seven or eight species of each area which are important in that area and characteristic of it are given on the accompanying maps⁴ (figs. 8-13).

The climax forest is the climatic type of the Cincinnati region, the range of the mapped species centering more or less about it. Thus the region is well within the mixed deciduous forest area of which this climax is representative. The canopy trees of the upland forest show a slightly more northern distribution, although the geographic ranges of the selected species differ but little from those of the climax. However, the understory plants of the pin oak forest show by their ranges a very decided northern relationship of this community.

The species from the prairie opening at Miamiville have the center of their general range much further west than that of the climax, the distribution more nearly coinciding with the great prairie region of the United States.

Perhaps more striking than any of the others are the affinities of the vegetation of the arid area. The center of the ranges for the eight character-

⁴ Distribution for shrubs and herbaceous plants mapped according to ranges given in *Illustrated Flora of the Northern States and Canada*, Britton and Brown, 2d ed., and in Gray's *New Manual of Botany*, 7th ed. Distribution for trees mapped according to ranges given in *Trees of the Northern States and Canada*, R. B. Hough, 1907.

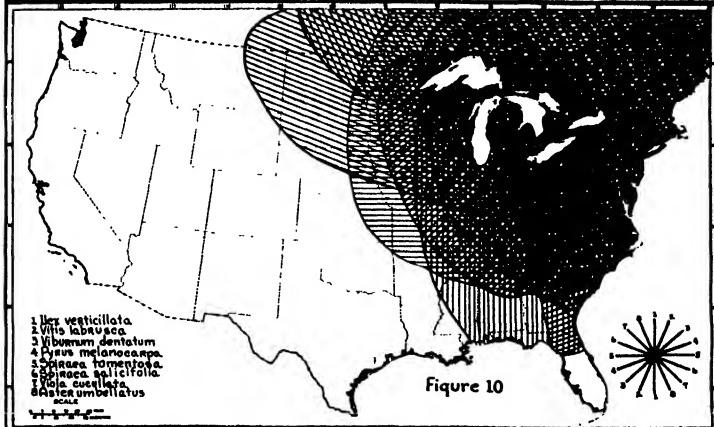
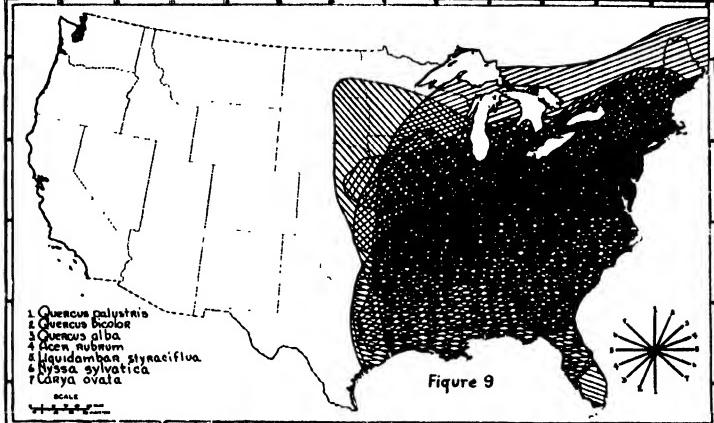
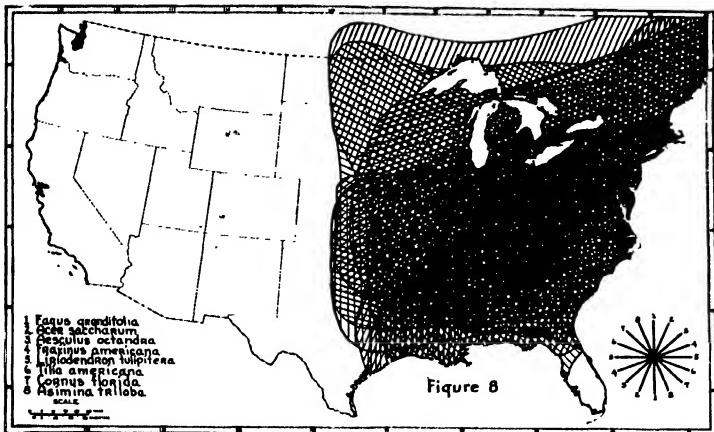


FIG. 8. Mesophytic climax forest. Geographic range of eight characteristic species. The numbers on the wheel spokes in the right-hand corner correspond to the species in the left; the direction of lines on the map indicates the designated species. The Cincinnati region is shown by the black star.

FIG. 9. Upland forest of pin oak type. Geographic range of seven characteristic species of the canopy.

FIG. 10. Upland forest of pin oak type. Geographic range of eight characteristic species of the understory.

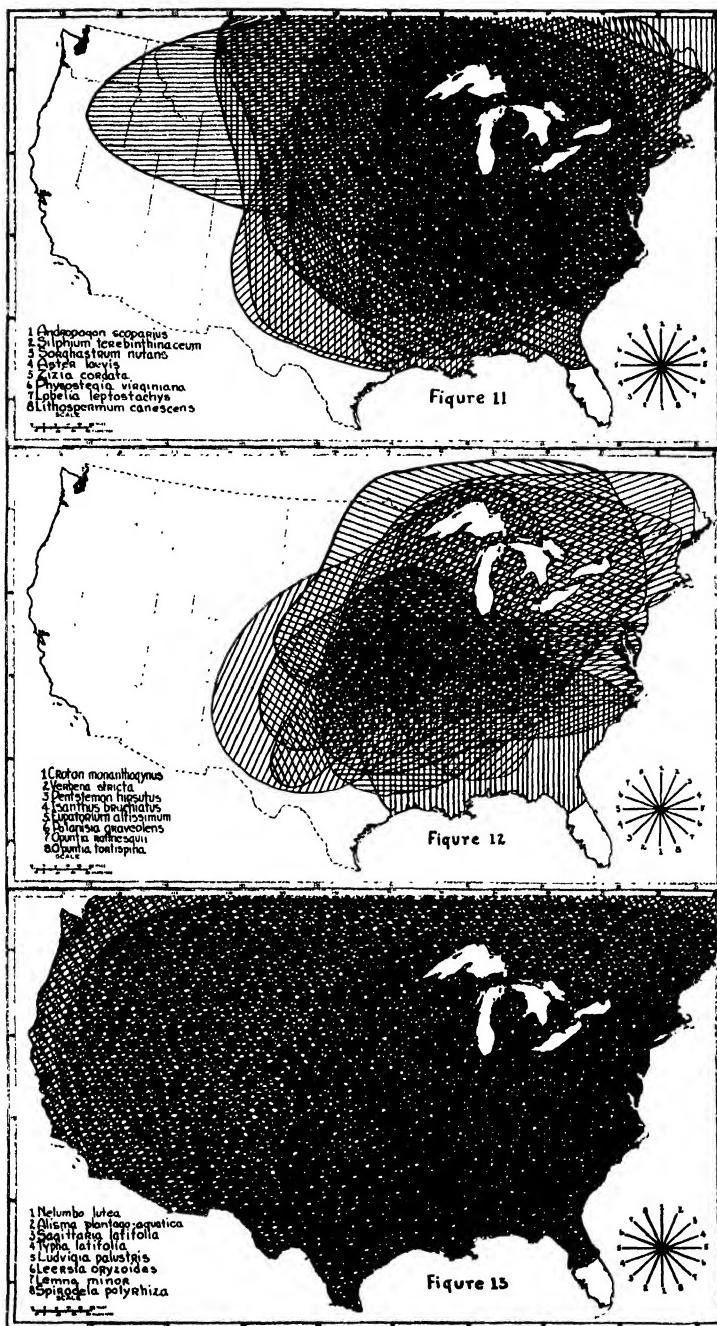


FIG. 11. Grassland community. Geographic range of eight characteristic species.

FIG. 12. Xerophytic community. Geographic range of eight characteristic species.

FIG. 13. Hydrophytic community. Geographic range of eight characteristic species.

istic and dominant species is very definitely in southwestern United States near the moister edge of the desert transition region.

The ranges of the aquatic and swamp species are very widespread, covering most of the United States.

The ranges mapped are in all cases very general in comparison with the actual occurrence of the species. The manuals include in the ranges given, not only the area in which the species is generally distributed, but also out-lying stations along the margin of its geographic range. Therefore, it is not to be thought that the ranges mapped include the area of continuous distribution but rather that near the margins, the species are of scattered occurrence while nearer the center of their ranges, the plants are apt to be widespread.

Methods

LIFE FORMS

Only a brief discussion is necessary concerning Raunkiaer's life form classification. Raunkiaer's groupings as designated by Fuller and Bakke (4) and Ennis (3) are used with the exception of the phanerophytic division. In the case of the phanerophytes, Raunkiaer's classes were found to be divided at heights which do not seem to coincide with the natural layering of forest vegetation. The life form groups used are defined below.

Phanerophytes are plants having their dormant buds on branches which project into the air and thus are woody plants. They may be further classified according to size, since this is determined by the relation between the plants and the humidity of the environment. The subgroups are: mega-phanerophytes, over 35 meters in height; macrophanerophytes, 15-35 meters; mesophanerophytes, 5-15 meters; microphanerophytes, 2-5 meters; nano-phanerophytes, under 2 meters. Divisions are also made as to the evergreen and deciduous character of the plants.

The chamaephytes include plants with their buds perennating on the surface of the ground or just above it (not exceeding 25 cm. above) so that in temperate and arctic regions they are protected by the snow, while in localities with a dry season some protection is afforded by plant remains. The buds are thus better protected than in the phanerophytes. This group is also divided as to evergreen and deciduous character.

The hemi-cryptophytes are plants with their dormant parts in the upper crust of the soil, just below the surface; the aerial parts are herbaceous in general and die away in the critical period although many have evergreen rosettes. These plants have been divided as to whether they are rosette plants or otherwise.

The cryptophytes are plants with their dormant parts entirely hidden. The three divisions of the cryptophytes are geophytes, helophytes, and hydrophytes. In case of the geophytes, there are bulbs, rhizomes, tubers and similar structures deep below the soil surface. The helophytes and hydro-

phytes are essentially marsh or water plants. Helophytes are those cryptophytes whose vegetative and floral shoots emerge from the water while hydrophytes are those whose vegetative parts are immersed or floating.

The therophytes are plants of the favorable season and live through the critical period as seeds and hence are annual plants.

Succulents are those plants which have fleshy stems or leaves, being either stem succulents or leaf succulents according to the part which is fleshy.

The great detail used by Ennis in her classification of geophytes and hemi-cryptophytes is omitted, as not necessary in order to designate the essential differences in the life forms of the species of the respective communities.

LEAF SIZE CLASSES

Raunkiaer's classes of leaf sizes are used, the following being the class size limits:

Leptophyll: 25 sq. mm. or less

Nanophyll: 25–9 × 25 sq. mm. (25–225 sq. mm.)

Microphyll: 9 × 25–9² × 25 sq. mm. (225–2,025 sq. mm.)

Mesophyll: 9² × 25–9³ × 25 sq. mm. (2,025–18,225 sq. mm.)

Macrophyll: 9³ × 25–9⁴ × 25 sq. mm. (18,225–164,025 sq. mm.)

Megaphyll: over 164,025 sq. mm.

The entire leaf rather than a leaf lobe or leaflet is used as the unit of measurement. Similarity of morphological structure and anatomical origin seems to justify this use. Parallel results are not obtained when the lobe of a leaf of one plant is measured, the leaflet of a second and the entire leaf of a third since a part of one leaf is not comparable to another leaf in its entirety in dealing with area limits. However, by measuring the whole leaf in all cases, comparable classification results. For example, *Cercis canadensis* and *Robinia pseudo-acacia*, both of which belong to the *Leguminosae* and take part at about the same stage in xerarch succession, would be in entirely different leaf size classes if the locust were classified on the basis of a leaflet as a unit and the redbud on the basis of its entire leaf. If, however, the entire leaf is measured in both cases, the leaves of the two species fall into the mesophyll class. The planimeter measurements of leaves of *Robinia* average 11,330 sq. mm. In the case of *Cercis* from the same locality, the average is 10,600 sq. mm.

In the case of the leaves of all the species, planimeter measurements were made of several leaves and the average taken for the classification.

Results

A list of the plants from the various communities and their classification as to life form and leaf size class are given on the following pages. In the

case of a plus or minus sign after the leaf size, doubt as to the classification is indicated, the plus showing a tendency toward the next larger size class and the minus the next smaller class. A classification into such intermediate groups as meso-microphyll, micro-nanophyll, etc. seems to be too detailed and complicated for the purposes of this investigation.

Mesophytic Climax Forest

PHANEROPHYTE

Megaphanerophyte

Liriodendron tulipifera.....	Meso ^b
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Macrophanerophyte

Acer saccharum.....	Meso	Prunus serotina.....	Meso
Acer saccharum nigrum.....	Meso	Psedera quinquefolia.....	Meso
Aesculus octandra.....	Macro	Quercus alba.....	Meso
Ailanthus glandulosa.....	Macro	Quercus macrocarpa.....	Meso
Carya cordiformis.....	Meso	Quercus muhlenbergii.....	Meso
Carya glabra.....	Macro	Quercus rubra.....	Meso
Celtis occidentalis.....	Meso	Rhus toxicodendron.....	Macro
Fagus grandifolia.....	Meso	Tilia americana.....	Meso
Fraxinus americana.....	Macro	Ulmus americana.....	Meso
Fraxinus quadrangulata.....	Meso+	Ulmus fulva.....	Meso
Gymnocladus dioica.....	Macro	Ulmus racemosa.....	Meso
Juglans cinerea.....	Macro	Vitis aestivalis.....	Meso
Juglans nigra.....	Macro	Vitis cordifolia.....	Meso

Mesophanerophyte

Asimina triloba.....	Meso	Cornus florida.....	Meso
Carpinus caroliniana.....	Micro	Morus rubra.....	Meso
Cercis canadensis.....	Meso	Ostrya virginiana.....	Meso
Cornus alternifolia.....	Meso		

Microphanerophyte

Benzoin aestivale.....	Micro	Rhus glabra.....	Meso
Celastrus scandens.....	Meso	Sambucus canadensis.....	Meso
Evonymus atropurpureus.....	Meso	Smilax hispida.....	Meso

Nanophanerophyte

Hydrangea arborescens.....	Meso	Rosa setigera.....	Meso
Rosa humilis.....	Micro		

CHAMAEPHYTE

Evergreen

Phlox divaricata.....	Micro
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Deciduous

Evonymus obovatus.....	Micro	Stellaria pubera.....	Micro-
Menispernum canadense.....	Meso	Valeriana pauciflora.....	Micro

^b The ending -phyll has been omitted from the leaf size class names.

HEMI-CRYPTOPHYTE

*Rosette*⁶

<i>Anemone virginiana</i>	Meso	<i>Polemonium reptans</i>	Meso
<i>Asarum canadense</i>	Meso	<i>Prunella vulgaris</i>	Micro
<i>Aster cordifolius</i>	Micro+	<i>Ranunculus abortivus</i>	Micro
<i>Aster shortii</i>	Micro	<i>Ranunculus micranthus</i>	Micro
<i>Camassia esculenta</i>	Meso	<i>Sanicula marilandica</i>	Meso
<i>Geranium maculatum</i>	Meso	<i>Senecio obovatus</i>	Micro
<i>Hepatica acutiloba</i>	Meso	<i>Solidago nemoralis</i>	Micro
<i>Heuchera americana</i>	Meso	<i>Stylophorum diphyllum</i>	Meso
<i>Hydrophyllum appendiculatum</i>	Meso	<i>Thalictrum dioicum</i>	Meso
<i>Hydrophyllum canadense</i>	Meso	<i>Viola papilionacea</i>	Micro
<i>Hydrophyllum virginianum</i>	Meso	<i>Viola pubescens</i>	Micro
<i>Jeffersonia diphylla</i>	Micro+	<i>Viola sororia</i>	Micro
<i>Lobelia siphilitica</i>	Meso	<i>Viola striata</i>	Micro
<i>Osmorhiza claytoni</i>	Meso	<i>Campanula americana</i> (B) ⁷	Micro
<i>Osmorhiza longistylis</i>	Meso	<i>Oenothera biennis</i> (B).....	Micro
<i>Phacelia bipinnatifida</i>	Micro	<i>Synandra hispidula</i> (B).....	Meso

*Protoheni-cryptophyte*⁸

<i>Aralia racemosa</i>	Macro	<i>Hybanthus concolor</i>	Micro
<i>Aster paniculatus</i>	Micro	<i>Isopyrum biternatum</i>	Micro
<i>Eupatorium altissimum</i>	Micro	<i>Monarda fistulosa</i>	Micro+
<i>Eupatorium urticaefolium</i>	Meso	<i>Phryma leptostachya</i>	Meso
<i>Galium circaeans</i>	Nano	<i>Polymnia canadensis</i> (Ch) ⁹	Meso
<i>Galium triflorum</i>	Nano	<i>Solidago latifolia</i>	Meso

CRYPTOPHYTE

Geophyte

<i>Anemonella thalictroides</i>	Meso	<i>Laportea canadensis</i>	Meso
<i>Aplectrum hyemale</i>	Meso	<i>Mertensia virginica</i>	Meso
<i>Arisaema dracontium</i>	Macro	<i>Obolaria virginica</i>	Nano
<i>Arisaema triphyllum</i>	Macro	<i>Orchis spectabilis</i>	Meso
<i>Claytonia virginica</i>	Micro	<i>Oxalis violacea</i>	Micro
<i>Collinsonia canadensis</i>	Meso	<i>Phytolacca decandra</i>	Meso
<i>Delphinium tricorne</i>	Meso	<i>Podophyllum peltatum</i>	Macro
<i>Dentaria diphylla</i>	Meso	<i>Polygonatum biflorum</i>	Micro
<i>Dentaria laciniata</i>	Micro	<i>Polygonatum commutatum</i>	Meso
<i>Dicentra canadensis</i>	Micro	<i>Sanguinaria canadensis</i>	Meso
<i>Dicentra cucullaria</i>	Micro	<i>Silene virginica</i>	Micro
<i>Epifagus virginiana</i>	Leafless	<i>Smilacina racemosa</i>	Meso
<i>Eriogonum bulbosa</i>	Nano	<i>Tradescantia virginica</i>	Meso
<i>Erythronium albidum</i>	Meso	<i>Trillium sessile</i>	Meso
<i>Erythronium americanum</i>	Meso	<i>Urtica dioica</i>	Meso

THEROPHYTE

<i>Collinsia verna</i>	Micro	<i>Impatiens pallida</i>	Meso
<i>Floerkea proserpinacoides</i>	Nano	<i>Pilea pumila</i>	Micro
<i>Galium aparine</i>	Nano		

⁶ All hemi-cryptophytes with basal leaves.⁷ Biennial.⁸ All hemi-cryptophytes without basal leaves.⁹ May be chamaephyte.

LEAF SUCCULENT

Sedum ternatum..... Nano

Upland Forest

PHANEROPHYTE

Macrophanerophyte

Acer rubrum.....	Meso	Prunus serotina.....	Meso
Acer saccharum.....	Meso	Quercus alba.....	Meso
Carya alba.....	Macro	Quercus bicolor.....	Meso
Carya ovata.....	Meso	Quercus imbricaria.....	Meso
Fagus grandifolia.....	Meso	Quercus palustris.....	Meso
Fraxinus americana.....	Macro	Quercus velutina.....	Meso
Juglans nigra.....	Macro	Quercus velutina missouriensis.....	Meso
Liquidambar styraciflua.....	Meso	Rhus toxicodendron	Macro
Nyssa sylvatica.....	Meso	Ulmus americana.....	Meso

Mesophanerophyte

Carpinus caroliniana.....	Micro	Salix discolor.....	Micro
Cercis canadensis.....	Meso	Sassafras variifolium.....	Meso
Cornus florida.....	Meso	Vitis bicolor.....	Meso
Pyrus coronaria.....	Micro		

Microphanerophyte

Evergreen

Juniperus virginiana..... Lepto

Deciduous

Amelanchier canadensis.....	Micro	Smilax glauca.....	Meso
Cephalanthus occidentalis.....	Meso	Smilax hispida.....	Meso
Corylus americana.....	Meso	Viburnum dentatum.....	Meso
Ilex verticillata.....	Micro	Viburnum prunifolium.....	Micro
Rhus copallina.....	Meso	Vitis aestivalis.....	Meso
Rhus glabra.....	Meso	Vitis labrusca.....	Meso

Nanophanerophyte

Hypericum prolificum.....	Nano	Smilax bona-nox.....	Meso
Pyrus melanocarpa.....	Micro	Spiraea salicifolia.....	Micro
Ribes cynosbati.....	Micro	Spiraea tomentosa.....	Micro
Rosa carolina.....	Meso	Vaccinium vacillans.....	Micro
Rosa setigera	Meso		

CHAMAEPHYTE

Evergreen

Mitchella repens..... Nano Rubus triflorus..... Meso

Deciduous

Evonymus obovatus..... Micro Stellaria graminea..... Nano

HEMI-CRYPTOPHYTE

Roselle

Hydrophyllum appendiculatum.....	Meso	Scirpus atrovirens.....	Meso
Krigia amplexicaulis.....	Micro	Scirpus lineatus.....	Meso

<i>Lobelia siphilitica</i>	Meso
<i>Polemonium reptans</i>	Meso
<i>Ranunculus hispidus</i>	Meso
<i>Ranunculus laxicaulis</i>	Micro

<i>Solidago aspera</i>	Micro
<i>Viola cucullata</i>	Micro
<i>Viola sagittata</i>	Micro

Protohemi-cryptophyte

<i>Asclepias quadrifolia</i>	Micro
<i>Bidens frondosa</i>	Micro
<i>Cinna arundinacea</i>	Meso
<i>Eupatorium perfoliatum</i>	Meso
<i>Galium triflorum</i>	Nano
<i>Phlox maculata</i>	Micro

<i>Pycnanthemum flexuosum</i>	Nano
<i>Scutellaria lateriflora</i>	Micro
<i>Steironema lanceolatum</i>	Micro
<i>Triosteum angustifolium</i>	Meso
<i>Myosotis virginica (B)</i>	Micro

CRYPTOPHYTE

Geophyte

<i>Agrimonia mollis</i>	Meso
<i>Arisaema dracontium</i>	Macro
<i>Aster umbellatus</i>	Micro
<i>Cardamine bulbosa</i>	Micro
<i>Claytonia virginica</i>	Micro
<i>Collinsonia canadensis</i>	Meso
<i>Dentaria laciniata</i>	Micro
<i>Epifagus virginiana</i>	Leafless

<i>Eupatorium maculatum</i>	Meso
<i>Habenaria peramoena</i>	Meso
<i>Oxalis violacea</i>	Micro
<i>Podophyllum peltatum</i>	Macro
<i>Polygonatum commutatum</i>	Meso
<i>Smilacina racemosa</i>	Meso
<i>Uvularia sessilifolia</i>	Micro

THEROPHYTE

<i>Galium aparine</i>	Nano
<i>Gratiola sphacrocarpa</i>	Micro
<i>Ilysanthes dubia</i>	Nano

<i>Impatiens biflora</i>	Meso
<i>Polygonum hastatum</i>	Meso
<i>Polygonum sagittatum</i>	Meso

Grassland

PHANEROPHYTE

Microphanerophyte

Evergreen

<i>Juniperus virginiana</i>	Lepto
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Deciduous

<i>Cercis canadensis</i>	Meso
<i>Juglans nigra</i> ¹⁰	Meso
<i>Quercus muhlenbergii</i>	Meso
<i>Quercus rubra</i>	Meso

<i>Rhus toxicodendron</i>	Meso
<i>Robinia pseudo-acacia</i>	Meso
<i>Ulmus americana</i>	Micro

Nanophanerophyte

<i>Lonicera dioica</i>	Meso
<i>Rosa humilis</i>	Micro

<i>Rosa setigera</i>	Meso
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CHAMAEPHYTE

Deciduous

<i>Aster laevis</i>	Micro
<i>Comandra umbellata</i>	Nano ¹¹

<i>Lobelia leptostachys</i>	Nano
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¹⁰ Trees which are of large size in the forest areas attain only a very small stature in the prairie due to unfavorable conditions for tree growth.

¹¹ Deep rootstock present.

HEMI-CRYPTOPHYTE

Rosette

<i>Anemone virginiana</i>	Meso	<i>Solidago ulmifolia</i>	Floral Micro
<i>Andropogon scoparius</i>	Micro		Basal Meso
<i>Aster cordifolius</i>	Micro	<i>Sorghastrum nutans</i>	Micro
<i>Hystrix patula</i>	Micro	<i>Thalictrum dioicum</i>	Meso
<i>Senecio obovatus</i>	Micro	<i>Viola sororia</i>	Micro
<i>Solidago nemoralis</i>	Floral Nano	<i>Zizia cordata</i>	Floral Micro
	Basal Micro		Basal Meso

Protohemicyclopedia

<i>Aster sagittifolius</i>	Micro	<i>Monarda fistulosa</i>	Micro
<i>Aster shortii</i>	Micro	<i>Solidago altissima</i>	Micro
<i>Convolvulus sepium repens</i>	Micro	<i>Solidago speciosa</i>	Meso
<i>Galium circaeans</i>	Nano	<i>Melilotus alba</i> (B).....	Nano
<i>Lepachys pinnata</i>	Micro		

CRYPTOPHYTE

Geophyte

<i>Allium cernuum</i>	Micro	<i>Physostegia virginiana</i>	Floral Nano
<i>Astragalus canadensis</i>	Micro		Basal Micro
<i>Euphorbia corollata</i>	Nano	<i>Silphium terebinthinaceum</i>	Macro
<i>Helianthus hirsutus</i>	Micro	<i>Silphium trifoliatum</i>	Micro
<i>Lithospermum canescens</i>	Micro	<i>Vincetoxicum obliquum</i>	Meso

THEROPHYTE

<i>Cassia chamaecrista</i>	Micro	<i>Gentiana quinquefolia</i>	Nano
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Xerophytic Community

PHANEROPHYTE

Microphanerophyte

<i>Prunus pumila</i>	Micro
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HEMI-CRYPTOPHYTE

Rosette

<i>Andropogon virginicus</i>	Micro	<i>Lactuca scariola</i> (B).....	Micro
<i>Pentstemon hirsutus</i>	Micro	<i>Oenothera biennis</i> (B).....	Micro
<i>Plantago lanceolata</i>	Micro	<i>Verbascum thapsus</i> (B).....	Micro
<i>Yucca filamentosa</i>	Meso		

Protohemicyclopedia

<i>Desmodium pauciflorum</i>	Meso	<i>Saponaria officinalis</i>	Micro
<i>Eupatorium altissimum</i>	Micro	<i>Verbena angustifolia</i>	Nano
<i>Kuhnia eupatorioides</i>	Micro	<i>Verbena stricta</i>	Micro
<i>Nepeta cataria</i>	Micro	<i>Melilotus alba</i> (B).....	Nano

THEROPHYTE

<i>Ambrosia artemisiifolia</i>	Micro	<i>Euphorbia maculata</i>	Lepto
<i>Arenaria serpyllifolia</i>	Lepto	<i>Geranium bicknellii</i>	Micro
<i>Bidens bipinnata</i>	Micro	<i>Isanthus brachiatus</i>	Lepto
<i>Cenchrus carolinianus</i>	Micro	<i>Oenothera laciniata</i>	Nano

<i>Croton capitatus</i>	Micro	<i>Polanisia graveolens</i>	Nano
<i>Croton monanthogynus</i>	Nano	<i>Polygonum convolvulus</i>	Micro
<i>Erigeron canadensis</i>	Nano	<i>Strophostyles helvola</i>	Micro
<i>Euphorbia dentata</i>	Nano	<i>Strophostyles pauciflora</i>	Micro

STEM SUCCULENT

<i>Opuntia rafinesquii</i>	Lepto	<i>Opuntia tortispina</i>	Lepto
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Hydrophytic Community**PHANEROPHYTE***Mesophanerophyte*

<i>Populus deltoides</i>	Meso	<i>Salix nigra</i>	Micro
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Microphanerophyte

<i>Salix longifolia</i>	Micro
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CHAMAEPHYTE

Deciduous

<i>Lysimachia nummularia</i>	Nano+
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HEMI-CRYPTOPHYTE*Rosette*

<i>Leersia oryzoides</i>	Micro	<i>Scirpus cyperinus</i>	Meso
<i>Prunella vulgaris</i>	Micro		

Protohemi-cryptophyte

<i>Ludwigia alternifolia</i>	Micro	<i>Lycopus virginicus</i>	Micro
<i>Ludwigia palustris</i>	Nano	<i>Mimulus ringens</i>	Micro
<i>Ludwigia polycarpa</i>	Nano	<i>Penthorum sedoides</i>	Micro
<i>Lycopus uniflorus</i>	Micro	<i>Scutellaria lateriflora</i>	Micro

CRYPTOPHYTE*Geophyte*

<i>Cyperus esculentus</i>	Micro
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Helophyte

<i>Alisma plantago-aquatica</i>	Meso	<i>Sparganium eurycarpum</i>	Meso
<i>Polygonum muhlenbergii</i>	Micro	<i>Typha latifolia</i>	Macro
<i>Sagittaria latifolia</i>	Meso		

Hydrophyte

<i>Callitricha heterophylla</i>	Lepto	<i>Nelumbo lutea</i>	Macro
<i>Ceratophyllum demersum</i>	Lepto	<i>Potamogeton dimorphus</i>	Nano
<i>Elodea canadensis</i>	Nano	<i>Spirodela polyrhiza</i>	Lepto
<i>Lemna minor</i>	Lepto	<i>Wolffia columbiana</i>	Lepto

THEROPHYTE

<i>Bidens aristosa</i>	Micro	<i>Eleocharis obtusa</i>	Leafless
<i>Bidens comosa</i>	Micro	<i>Ranunculus sceleratus</i>	Micro
<i>Echinochloa crusgalli</i>	Micro	<i>Strophostyles helvola</i>	Micro

TABLE I. Life form percentages of five communities of the Cincinnati region

Community	Phanerophyte												Cryptophyte												Succulent			
	Chamaephyte				Hemi-Cryptophyte				G				HE				HY				Therophyte							
	MM	M	MS	MC	N	E	D	R	P	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
Climax mixed mesophytic forest.....	1	.78	26	20.3	7	5.5				3	2.3	1	.78	4	3.1	32	25.	12	9.4	30	23.4							
Upland forest.....		18	19.1	7	7.4	1	1.06	12	12.7	9	9.5	2	2.1	2	2.1	11	11.7	11	11.7	15	15.9	5	3.9					
Grassland.....										7	15.5	3	6.7	3	6.7	11	24.4	9	20.	9	20.	2	4.4					
Xerophytic community.....										1	2.94					7	20.6	8	23.5			16	47.	2	5.9			
Hydrophytic community.....										1	2.86			1	2.86	8	22.9	1	2.86	5	14.3	8	22.9	6	17.2			

MM—Megaphanerophyte
M—Macrophanerophyte
MS—Mesophanerophyte
MC—Microphanerophyte
N—Nanophanerophyte
R—Rosette

P—Protohemicyclopedia
G—Geophyte
HE—Helophyte
HY—Hydrophyte
E—Evergreen
D—Deciduous

Comparison of Communities and Correlation with Geographic Formation

The tabulated results indicate in a general manner the great differences exhibited by the various communities as to life form and leaf size classes. The percentage tables I and II and graphs (figs. 14, 15, 16) bring out these differences in a more striking manner.

TABLE II. Leaf size class percentages of five communities of the Cincinnati region

Community	Macro-phyll		Meso-phyll		Micro-phyll		Nano-phyll		Lepto-phyll		Mixed		Leafless	
	No.	%	No.	%	No.	%	No.	%	No.	%	Nano-Mic.	Mic-Mes.	No.	%
											No.	%		
Climax mixed mesophytic forest	12	9.4	72	56.1	36	28.1	7	5.5					I	.78
Upland forest	6	6.4	49	51.9	30	31.8	7	7.4	1	1.06	2	4.4	1	1.06
Grassland	1	2.2	12	26.6	21	46.6	6	13.3	1	2.2				
Xerophytic community			2	5.9	20	58.8	7	20.6	5	14.7				
Hydrophytic community	2	5.7	5	14.3	17	48.6	6	17.2	4	11.4			I	2.86

LIFE FORM

In considering the life forms and their significance, it perhaps would be the best course to review previous work done on life forms and their correlation with definite vegetation regions. According to Raunkiaer (4, 7), temperate regions with a moderate dry season are characterized by a hemi-cryptophytic vegetation. Phanerophytes are directly connected with the moisture conditions; the greater the amount of available moisture, the greater the number and size of the phanerophytes. Ennis' investigation (3) concerning the life forms of the Connecticut flora substantiates Raunkiaer's findings. She states that 49.4 per cent of the entire flora of Connecticut falls into the hemi-cryptophytic class with phanerophytes important as to life form and physiognomy.

Investigations of Paulsen (6) on the short grasslands of the United States show that the areas are predominantly hemi-cryptophytic with the phanerophytes in a definite minority. He also found that the flora of certain North American deserts is prevailingly therophytic. Raunkiaer, too, classifies desert vegetation as being predominantly annual.

The climax forest of the Cincinnati region, as indicated on the preceding pages, is primarily hemi-cryptophytic as to life form although its physiognomy is phanerophytic. However, the phanerophytes are almost as abundant as to number of species, with the macrophanerophytes prevailing. These results are well correlated with Raunkiaer's climatic groupings of

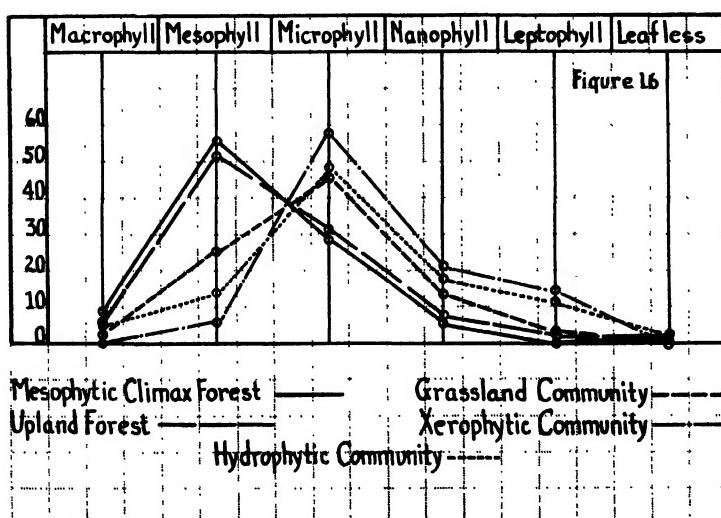
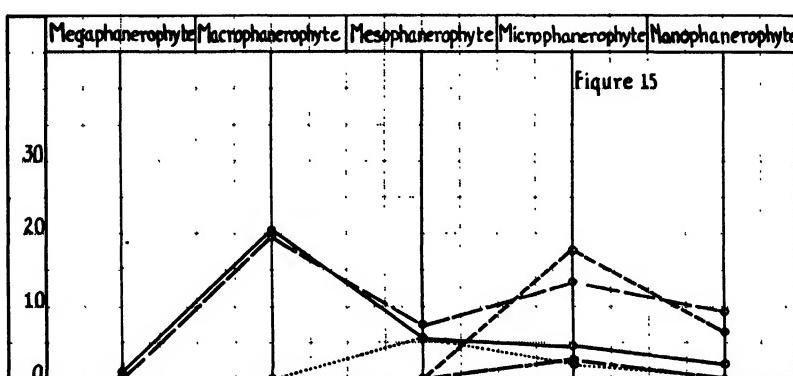
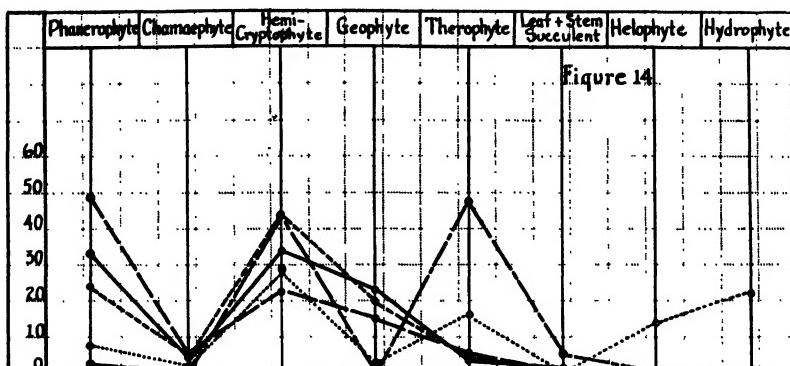


FIG. 14. Graph of life form percentages of five communities of the Cincinnati region.

FIG. 15. Graph of phanerophyte percentages of five communities of the Cincinnati region.

FIG. 16. Graph of leaf size class percentages of five communities of the Cincinnati region.

hemi-cryptophytes and phanerophytes, the climatic vegetation being very directly connected with the climate which is moderate as to temperature and rainfall.

The upland forest is characterized by a large percentage of phanerophytes with a larger number of shrubs than is present in the climax. Hemi-cryptophytes are next in rank although the percentage of these is more than 10 per cent lower than in the climax forest. The upland forest has less herbaceous undergrowth than has the climax as is evidenced by the lower percentage of hemi-cryptophytes and geophytes. The low percentage of geophytes is in all probability due to the saturated soil conditions in the pin oak forest. The greatly decreased percentage of herbaceous plants of the undergrowth and a predominance of shrubs is very characteristic of more northern vegetation. In this connection, it will be noted that the shrubs of this forest show decided northern affinities in their geographic distribution.

The prairie opening at Miamiville is essentially hemi-cryptophytic in nature, over 44 per cent of the species being of this class. It seems at first glance that the number of phanerophytes is large for the type of vegetation. However, the percentage is based on number of species and not of individuals. There is a fair number of species coming into the opening from the surrounding forest area with only a very few individuals of each species present. A frequency correlation of individuals with species would probably show the true relationship of the phanerophytes to the mass vegetation. Otherwise the percentages fit well with the results obtained by Paulsen and the number and size of the phanerophytes show a relationship to the moisture conditions indicated by Raunkiaer. Definite life form affinities of the opening to the western grassland are shown which, together with the similarity of species and physiognomy, point clearly to a close relationship of the two as indicated by the center of the geographic range of the characteristic species. It should be noted that Paulsen's work is on the short grass plains while the Miamiville opening is tall grass.

The "desert" terrace area species are about 47 per cent annual with a large percentage of hemi-cryptophytes, about 12 per cent of the latter being biennial. Here again is a striking correlation. Investigation of life forms of the desert vegetation of the United States by Paulsen indicates that the species are 42-47 per cent annual. In comparing the ranges of the characteristic species, a relationship to the arid southwest is shown.

The hydrophytic community shows a large percentage of helophytes and hydrophytes which together take in over 35 per cent of the species. There is also a large percentage of hemi-cryptophytes which may be directly correlated with the temperate climate and an unfavorable season which is not too severe.

LEAF SIZE CLASS

A great variation in the percentage of leaf size classes from community to community is evidenced by the vegetation types observed. It will be

noted from table II and the graph (fig. 16) that both of the forest types are characterized by leaves of mesophyll size, with a larger percentage of microphyllous leaves in the upland forest than in the climax. In the forests there is a larger percentage of species with macrophyll leaves than in any of the other communities while in both cases there are no leaves smaller than those of the nanophyll class with the exception of *Juniperus virginiana* in the upland forest.

The grassland area has a small percentage of macrophyllous leaves while the greatest number of species belong to the microphyll class. A fair percentage of mesophylls is present. There is a noticeable increase in the percentage of small leaf size classes in the prairie area as compared with the forest areas.

The arid terrace is also predominantly microphyllous; there are no plants with macrophyll leaves and only a few with mesophylls. There is a large percentage of nanophylls and leptophylls.

The hydrophytic community is prevailingly microphyllous, although there is a small percentage of macrophylls and a moderate percentage of mesophylls. A number of species belonging to the smallest leaf size classes is also present. This group shows a more even distribution of species in all the classes than is found in any of the other communities.

The above results indicate that with an increase of xerophytism there is a decrease in the percentage of large leaf size classes and an increase in the smaller ones. Thus, the forests have the greatest percentage of large leaf size classes, the grassland has a lesser percentage of large leaf sizes and an increased number of species with leaves belonging to the smaller sizes, while the "desert" has the greatest percentage of small leaf size classes.

These results seem to be well correlated with the geographic relationships as exhibited by the ranges of the characteristic and dominant species of each area and by the life form percentages as indicated above.

Summary

1. Within the Cincinnati region are present several diverse communities of which five were investigated, *i.e.*, the climax forest, the upland forest, a prairie opening at Miamiville, a xerophytic community and a hydrophytic community.

2. From the classifications of the flora of each of these communities according to Raunkiaer's life forms and leaf size classes and a mapping of the geographic ranges of eight characteristic and dominant species (seven in one case) of each area, the following conclusions have been drawn concerning the vegetation of each of these communities:

a. The flora of the climax forest is prevailingly hemi-cryptophytic with a large percentage of phanerophytes, macrophanerophytes dominating. The leaf sizes are predominantly mesophyllous with a very small percentage of

small leaf size classes. This vegetation type is thus well correlated with the climate.

b. The upland forest vegetation is principally phanerophytic with a great number of hemi-cryptophytes. There is a larger number of micro- and nanophanerophytes than in any of the other areas, with a decreased number of species in the herbaceous classifications. The upland forest is prevailingly of a mesophyll nature according to leaf size classes with a greater percentage of microphyll leaves than is present in the climax forest. According to life form percentages and the geographic ranges of the characteristic species, a rather northern affinity is exhibited.

c. The grassland area is primarily hemi-cryptophytic with a greater number of species belonging to the microphyll leaf size class. According to results obtained, the life form percentages are directly correlated with the western grassland as evidenced by the geographic ranges of the mapped species while the leaf size class percentages indicate an increase of xerophytism over the forest areas.

d. A definite relationship of the xerophytic community to the drier regions of the United States is shown by the 47 per cent therophytic life form. The microphyll leaf size class contains the greatest number of species with a large percentage of the two smallest leaf size classes present, indicating a more xerophytic condition than is shown in any of the other areas. This is definitely related to the distribution of the characteristic species which shows the center of their ranges to be near the arid southwestern desert-grassland transition region of the United States.

e. The hydrophytic community shows no definite relationship to any region on which any detailed work on life forms has been done. Such communities are of course edaphic rather than climatic, hence relationship to a climatic region is not to be expected. The widespread geographic distribution of the hydrophytes also shows their independence of climatic regions. The helophyte-hydrophyte group is most important; hemi-cryptophytes are next. The predominant leaf size class is the microphyll although the leaf sizes show a more even distribution in all the classes than is found in any other community.

Note: The work for the preparation of this article was done in the Department of Botany, University of Cincinnati, under the direction of Dr. E. Lucy Braun, who has offered valuable suggestions and who devised the system of mapping used in this paper to indicate the geographic range center for certain groups of characteristic species.

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ENVIRONMENT AND CROP PRODUCTION IN OREGON

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The relation of environment to the types of crop plants grown is marked. The effect of environment on texture, color, succulence and other quality factors is common knowledge. This is particularly true in Oregon where there are several distinct sets of climatic conditions and a large variety of crops. A study of these relationships involves both plant ecology and agronomy. Their connection was brought out by Dean Coffey of Minnesota who recently quoted this definition of agronomy, "If I were to try to surround agronomy with one all inclusive term I would say that it might be a matter of plant ecology which has very definite economic implications."

The comparatively recent interest of ecologists in economic plants and the recent increased interest of agronomists in the plant and its environment, indicate that the solutions of many of our puzzling problems in the culture of field crops may be found in ecological studies. Problems of irrigation, shading, length of day, tillage and winter injury should be studied from the environmental point of view. Agronomists are showing a re-awakened interest in plant ecology and I believe that they will contribute much to the literature of ecology, particularly from the standpoint of field plat technique and its application to results. A thorough study of the relation of climatic cycles to crop yields and crop diseases would reveal interesting and valuable information.

A preliminary study of environment and crop production in Oregon has led to this contribution. There are more than sixty millions of acres of land in Oregon. Only about twenty-seven million acres, however, are assessed on the tax rolls. The remainder of the land is included in forest reserve, unappropriated and unreserved land, town lots and water sheds. About three million acres are in crops of various kinds.

The last census showed that there were slightly more than fifty-five thousand farms and about a million people in the state. These figures indicate vast areas, few farms and scattered population. This fact is emphasized when it is known that the city of Portland alone has one-third of the population.

The study of crop ecology in Oregon is of unusual interest because there are few areas in the United States which have such a wide range of environmental conditions. The Pacific Ocean on the west, the high, dry plateaus of an elevation of more than 4,000 feet on the east, and the various mountain ranges create striking differences in climate. Altitudes vary from sea level to 12,000 feet above. Crops such as rye are grown at an altitude of 8,000

feet. Along the coast, frost and snow are infrequent and, on the other extreme, high temperatures are uncommon. In some sections, such as Coos Bay, it is so mild that palm trees are grown and grass grows the year around. In certain agricultural sections in the central part of the state, frost occurs every month in the year and some of the mountain peaks are covered with perpetual snow. Rainfall ranges from more than 100 inches on the west coast to less than 10 inches in Eastern Oregon. The seasonal distribution of this rainfall is striking in that most of it, in both sections of the state, is in the fall and winter. These varied conditions complicated with variations in soil type present interesting ecological problems.



FIG. 1. Picking cranberries in coastal area of Oregon. A crop typical of this low, wet acid soil condition.

The soils of a region are chiefly the result of environmental conditions. The soils of Oregon are extremely variable. In general, much of the soil forming material is derived from lava which covered a large portion of the state. In the western part of the state the soils tend to be acid, some with a pH of 4.5. Eastern Oregon soils are neutral to alkaline in reaction and where the water table is high "alkali spots" are fairly common. Soil reaction follows rainfall fairly closely. Acid soils are usually not found where rainfall is below 30 inches. On the other hand, such soils are fairly common where the rainfall is above 40 inches. Heavy rainfall, 40 to 100 inches, as found on the Oregon coast, develops extreme acidity and the ordinary legumes are not grown except where heavy applications of lime are made. Detailed soil surveys of these areas have been made only in the Willamette Valley.

For this study, the state is divided into two large divisions, eastern and western Oregon. In turn each of these divisions is subdivided into three sections, making six physiographic areas. These six areas are described in the following paragraph:



FIG. 2. Oregon is the leading hop state. This crop is an indicator of conditions in the Willamette Valley area.



FIG. 3. Southern Oregon is a pear crop area because of a peculiar combination of climatic and soil conditions.

Beginning on the west with the rugged Pacific Coast shore line, there is a small agricultural region (see Fig. 1) varying in width from a few miles to forty or fifty and known as the coast district. The eastern boundary of this district is the Coast Range which varies in altitude from a few hundred feet to about 4,000 feet above mean sea level. Just east of the Coast Range there is the Willamette Valley of large size and composed of a group of small valleys rather than a single one. This valley embraces the northern part of this western division. The southern part of the district between the Coast and Cascade Ranges of mountains is known as the Southern Oregon area

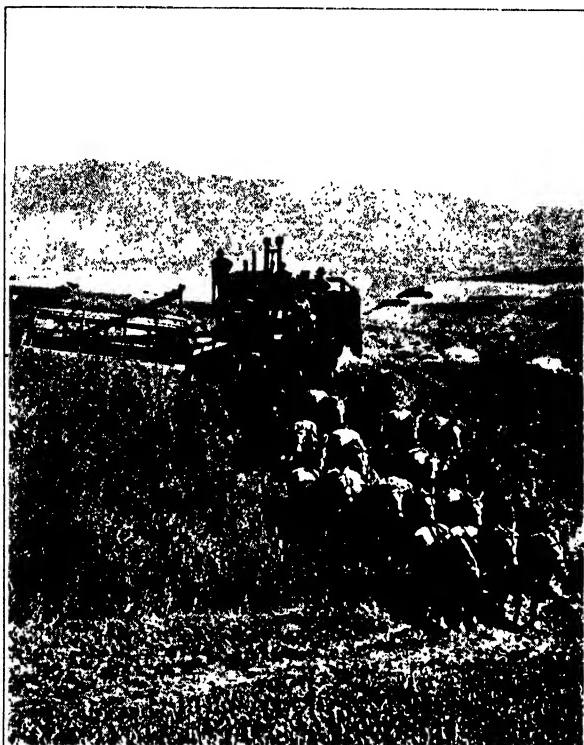


FIG. 4. Winter wheat on summer fallow is typical of the Columbia Basin area of Oregon.

and has characteristics quite different from the Willamette Valley and so it is treated as a third area (see Fig. 3). This entire division is sometimes referred to as Western Oregon in distinction from Eastern Oregon which lies on the eastern side of the Cascade Range.

Eastern Oregon is divided into three main areas. The great Columbia Basin (see Fig. 4), occupying the northern part of the central section of the state, is the most important agricultural division of the eastern part of Oregon. To the east of the Columbia Basin area is the Blue Mountain area, the agricultural part of which consists chiefly of high valleys. The third and

largest crop area is called Central Oregon and occupies all of the south-eastern part of the state and nearly one-half of the state's area.

While Western Oregon is noted for a wide variety of conditions, featured chiefly by mild and moist winters, Eastern Oregon has low precipitation and humidity, high evaporation and wind velocity, considerable sunshine, extremes of temperature, and other conditions characteristic of arid regions.

Now what are the chief crops of each area and do any of these crops indicate certain environmental conditions?

Beginning on the west with the coastal area we find some interesting crops not generally grown in other agricultural regions. Some of these are



FIG. 5. Hay and grain are the common crops in the Blue Mountain area of Oregon.

rutabagas, turnips, cranberries, native bent grasses (*Agrostis*) and Japanese millet (*Echinochloa*). The cranberry bog shown in Fig. 1 is characterized by vegetation typical of this area. In Oregon these crops are associated with the mild, moist climatic conditions which dominate this coastal area.

Nearly all field crop plants except a few of those typical of the cotton belt, such as tobacco and cotton, and even these can be grown, are found in the Willamette Valley. A great diversity of crops suggests mild conditions, but the lack of certain strictly southern crops indicates that summer conditions may not be warm and moist as in the South. In fact the Willamette Valley is cool and dry during the summer. Some of the "unusual" crops in this area are hops, peppermint, pyrethrum, and teasels. Hop picking as shown in Fig. 2 is a common scene in this area. Rutabagas, turnips, bent grass seed and Japanese millet mentioned as characteristic of the adjacent

coast area are not commonly grown in the Willamette Valley, indicating a different environment.

The area known as Southern Oregon is chiefly an irrigated section with fruit and alfalfa. The abundance of pears (see Fig. 3) in this area shows that the winters are mild and the soil is too heavy for apples and other fruits. Southern Oregon is thus different from many irrigated areas where cold winters predominate and soils are of lighter types.

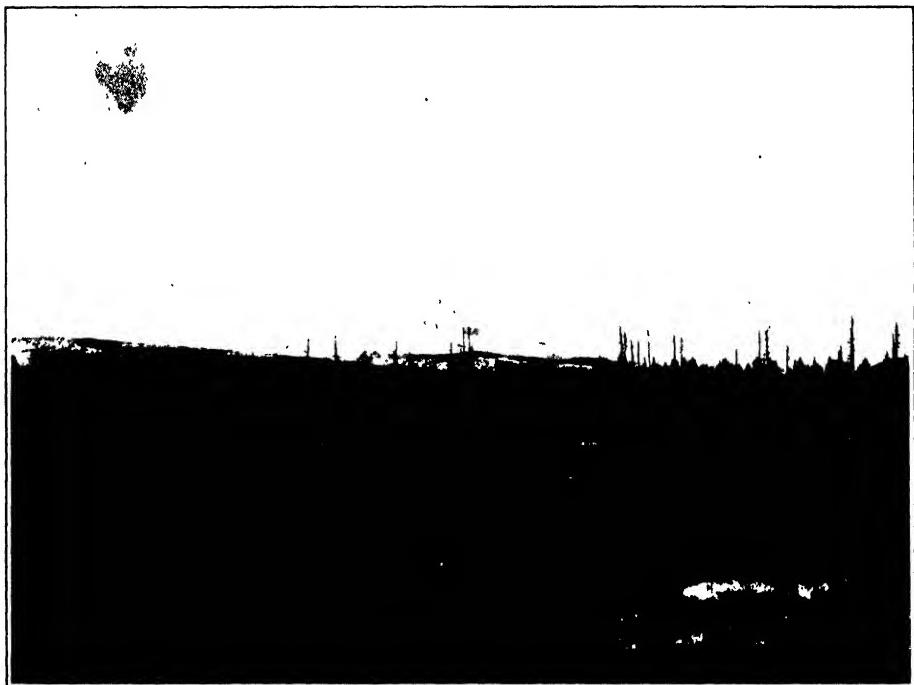


FIG. 6. The cattle industry of central Oregon is founded on these high mountain meadows. Most of the remainder of this area is a dry plateau.

Of these several areas, the Columbia Basin area is one of the most outstanding. A summer fallow system of growing winter wheat on large farms indicates low rainfall and low humidity associated with severe conditions such as high wind velocity and extremes of temperature.

The Blue Mountain area is characterized by alfalfa, pastures, potatoes, clover seed, spring grain, sunflowers, and other hardy crops. This diversification of crops indicates small farms, irrigation, cold winters, and short seasons. A typical scene in one of the small valleys in this area is shown in Fig. 5.

The absence of many common field crops in Central Oregon outside of a few irrigated sections means low rainfall—less than ten inches. Hardy crops

such as spring oats and rye indicate the extreme aridity of this area. The high mountain meadows as shown in Fig. 6 are also characteristic of this area.

Perhaps the relation between ecological factors and kinds of field crops in Oregon is more striking to one familiar with the state and its crops. These examples have been used, however, to bring out the importance of the application of ecological principles to the solving of agronomic problems. I hope that this brief study will be a stimulus to other agronomists in the analysis of the crop areas in the various states.

POPULATIONS OF WHITE GRUBS IN PASTURES WITH RELATION TO THE ENVIRONMENT*

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Many of the permanent blue grass pastures of southern Wisconsin have suffered regularly from attacks of white grubs (*Phyllophaga* spp.) with a climax in 1930 of the heaviest injury ever experienced (Fig. 3). The entire territory is generally infested and many pastures have been almost completely ruined although within this area there are fields or parts of fields which show little or no apparent injury. These particular fields have remained fairly productive throughout the past year even with a general lack of sufficient rainfall.

Preliminary observations have shown that the uninjured areas were of three general classes—narrow valleys or ravines, virgin pastures judiciously grazed, and pastures known to be relatively high in fertility which at the same time had not been grazed too early or too closely. Injured areas were either in fields low in fertility, such as the hillsides where the soil was thin and dry due to outcroppings of limestone, or in fields where it was known that over-grazing had been practiced.

Graber, Fluke, and Dexter¹ have shown that in controlled cultures of blue grass (*Poa pratensis*) any factor or group of factors of the external and internal environments, limiting the amount of subterranean growth and the regenerative capacity of the grass intensifies the degree of injury sustained from approximately equal numbers of grubs introduced in such cultures. It is the purpose of this paper to indicate that under field conditions a similar relationship holds, but in addition, a generally favorable environment for the grass reduces the infestations of the insect. Such conclusions were drawn from actual counts of the numbers of grubs in several permanent blue grass pastures where a knowledge of the soil fertility, previous grazing practices, and general moisture conditions, was available.

Very little definite evidence has been published on the oviposition activities of June beetles (also known as May beetles). An important contribution is a paper by Sweetman.² He surveys the literature on the subject and

* Contribution from the Departments of Economic Entomology and Agronomy. Published with approval of the Director of the Wisconsin Experiment Station.

¹ Graber, L. F., Fluke, C. L., and Dexter, S. T., Insect injury of blue grass in relation to the environment. *ECOLOGY*, 12: 547-566.

² Sweetman, Harvey L. 1927. A preliminary report on the factors controlling the oviposition of May beetles in Minnesota. *Jour. Econ. Ent.*, 20: (6), 783-794. Figs.

the reader is referred to his paper for a review of the previous work on this problem. Sweetman concludes that "May beetles do not select places for oviposition according to the vegetational covering but fly at random from the food plants. . . . Oviposition is in the immediate vicinity of food plants regardless of the elevation or type of soil *when the physical conditions are suitable.*" (Authors' italics.) . . . "Egg laying can be delayed at least 5 days when the bettles chance to get into unfavorable places. Probably many eggs and young grubs are destroyed in very dry soils." He also states that

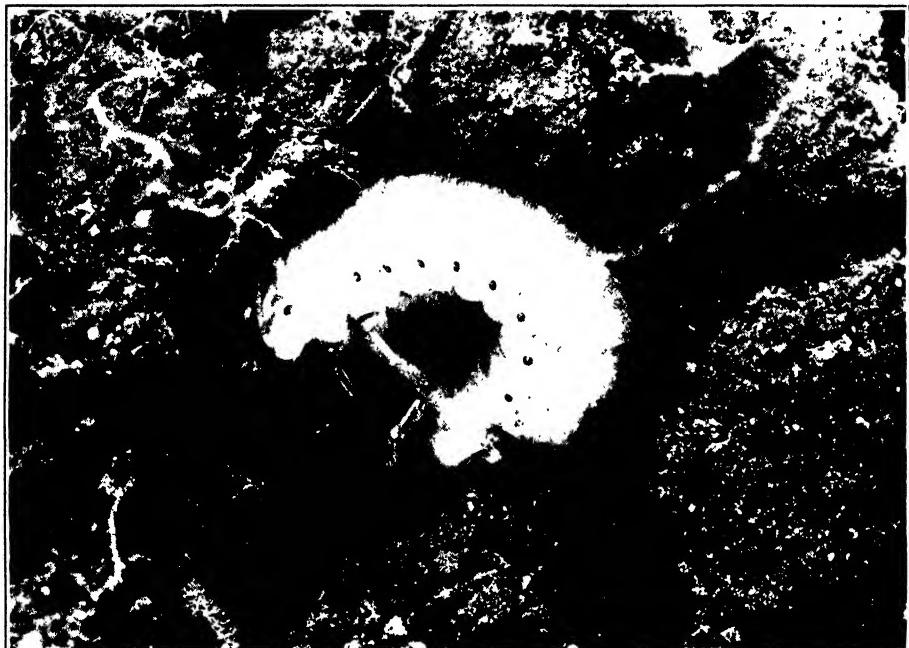


FIG. 1. A white grub (enlarged 4 times)—it is the larva of June beetles (*Phyllophaga* spp.). The larvae consume the subterranean growth of plants such as pasture and hay grasses, small grains and corn.

"the type of vegetation may sometimes be a factor in keeping the beetles out. Bent grass, (*Agrostis stolonifera*) on a Minnesota golf green was found to prevent *P. rugosa* from burrowing in the sod because of the thick root matt."

The results to be reported in this paper seem to show that Sweetman's statement regarding the prevention of burrowing of *P. rugosa* because of the thick root mat, is the most important factor involved in the relative freedom from grubs of certain pastures in Wisconsin.

THE LIFE CYCLE OF WHITE GRUBS

In order to fully understand the population studies, it is well to describe briefly the life history of white grubs as they exist in Wisconsin. Sanders

and Fracker³ found and identified 17 distinct species of June beetles in southern Wisconsin although a number of these were taken very rarely. The majority of the species have a three year life cycle and belong to "Brood A," the adults of which appeared in 1926, 1929, and normally, will fly again in 1932. The eggs are deposited during the flight and hatch soon after. The grubs feed for the balance of the season and continue through the second season when as a result of their rapid feeding and growth, damage is greatest (Figs. 1 and 3). In the third year the grubs feed only a short time, pupating in early summer and changing to adults by fall. They remain in the soil over winter, emerging the next spring when the cycle starts over.

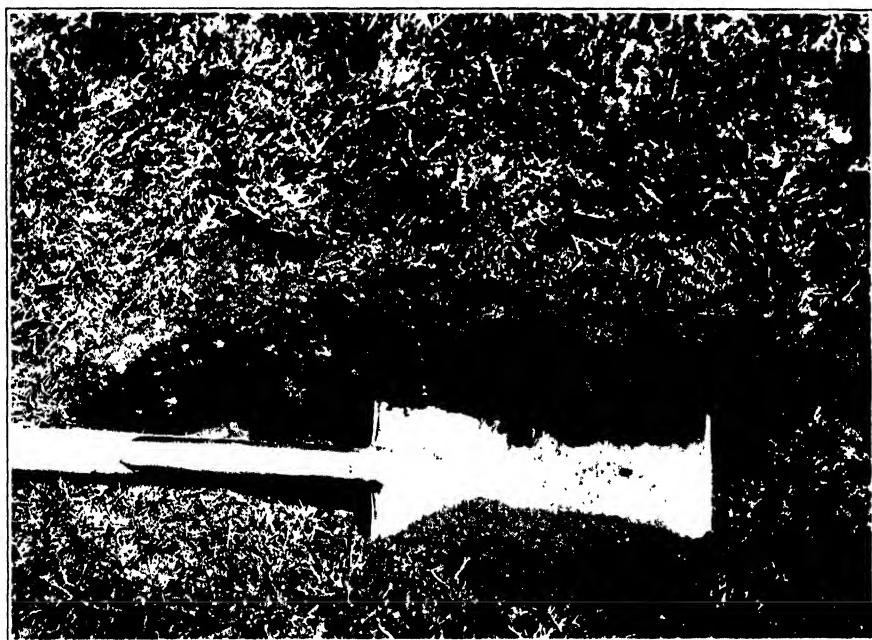


FIG. 2. This thick dense grass sod resulted from abundant fertilization, judicious grazing, and generally favorable moisture conditions. There were relatively few white grubs found in or beneath sods with such an environment.

METHOD OF DETERMINING WHITE GRUB POPULATIONS

The unit of measurement selected was one twenty thousandth of an acre, which is just slightly larger than two square feet. A small rectangle made of wood, the inner edge of which measures the exact area, was placed on the grass and with the aid of a corn knife and a spade the sod was cut and lifted. Very heavy turfs were cut up into four smaller pieces. The grubs were removed from the cakes of sod and from the soil to a depth of approximately

³ Sanders, J. G., and Fracker, S. B. 1916. Lachnosterna records in Wisconsin. *Jour. Econ. Ent.*, 9: 253-261

six inches. The majority of the grubs were found in the upper three or four inches. Nearly a thousand counts were made and are summarized in the accompanying table.

The injury occasioned by grubs in pastures had become so acute that definite plans were made early in the year (1930) to study the problem from all angles. Many outstanding contrasts of grub injury were evident. Oftentimes a nearly complete destruction of grass occurred in one pasture only to find another just across the fence showing almost no signs of grub injury. Such peculiar situations in neighboring pastures gave rise to a number of questions among investigators as well as among the farmers.

POPULATIONS OF WHITE GRUBS

At the beginning of the study four main combinations (see table) of existing pasture conditions were noted. Pastures with these factors apparent were chosen and grub populations determined. One group of such pastures were in excellent condition, with heavy sods, so intertwined with roots and rhizomes that they were pulled apart with difficulty. This type

POPULATIONS OF WHITE GRUBS IN PERMANENT BLUE GRASS PASTURES IN SOUTHERN WISCONSIN, 1930

Series no.	Description of grassland	No. of counts	Total no. of grubs	Ave. no. of grubs per count	No. of grubs per acre
1	Thick, heavy turf, and favorable soil—21 areas	314	1,110	3.53	70,600
2	Thin turf and poor soil—24 areas.....	269	2,767	10.29	205,800
3	Hillsides—thin dry soils—4 areas.....	79	763	9.7	194,000
4	Narrow valleys or shallow ravines—moist soil—4 areas.....	48	124	2.6	52,000
5	Virgin sod—no cropping—2 areas.....	37	189	5.1	102,000
6	Non-virgin sod—cropped heavily before blue grass became established—2 areas.....	34	367	10.9	218,000
7	Blue grass adjacent to sweet clover in Series 8—5 areas.....	62	457	7.4	148,000
8	Sweet clover—growing in blue grass pastures during beetle flight of 1929—5 areas.....	66	89	1.4	28,000

of turf (Series 1), varied from one to three inches in thickness, and manifested no visible signs of injury. On the other hand the pastures badly injured had poor or very thin sods, fewer roots, less rhizomes and considerable soil (Series 2) was exposed between the tufts of grass.

The grub counts in these two types of pastures showed that there were only about one-third the number of grubs in the thick sods as occurred in the thin sods. Of the 314 counts made in good pastures with thick sods 1,110 grubs were found, giving a rate of 70,600 per acre while 269 counts in poor pastures with thin sods revealed 2,767 grubs or 205,800 per acre. It should be stated that the grubs feed mostly on a horizontal plane just be-



FIG. 3. This area was near that shown in Fig. 2 and was abundantly infested with white grubs. The sod was thin due to a lack of fertility in the soil.



FIG. 4. The pasture on the right had been well fertilized prior to the beetle flight of 1929 and escaped severe injury from the white grubs while the sod on left without fertilization was severely injured, as shown by the lighter color of the dead grasses.

neath the turf so that the thickness of sod can be ascertained even after considerable injury has occurred.

Thus a contrast of injured and uninjured grasses was often found adjacently in large pastures separated only by a fence (Figs. 4 and 5). The pastures with few grubs were invariably those with relatively high fertility and which had not been grazed excessively nor too early. The production of a heavy turf by these favorable conditions either caused the beetles to seek elsewhere to lay or if the eggs were laid, they or the newly hatched grubs died before penetrating the soil. Figure 2 illustrates a heavy thick turf and Fig. 3 shows an exceedingly thin turf which has been completely severed by grubs from its soil contacts.



FIG. 5. The blue grass pasture in foreground is fully forty years old. The soil is exceedingly fertile and the grass has been judiciously grazed resulting in a heavy dense sod which was not injured by white grubs. The grass (mostly timothy) in the less fertile hay field (on right) was mostly destroyed by the abundant infestation of white grubs.

Red clover (in background) was not injured.

Many blue grass pastures which did not show any evidences of grub infestations contained often as many as 80,000 to 90,000 grubs per acre. With a favorable environment the grasses in these pastures were able to regenerate sufficient new growth to withstand the attack of the insects. Thus a heavy turf not only tends to prevent excessive numbers of grubs but it also tends to outgrow the attacks of those which do gain a foothold.

The second combination of pasture conditions was found in the hilly sections. The hillsides or steeper slopes have considerable outcroppings of limestone and as a result the sod is often thin. This condition is also aggravated by a relatively inefficient moisture content in such soils especially

during dry seasons. A very good sod, however, was found in the narrow valleys or ravines at the base of these slopes and such areas were usually free from grub damage.⁴ The soils in these valleys are higher in fertility and in moisture content. They are usually quite moist in the spring during egg laying time. An environment with considerable moisture especially to the point of free water would very likely be unfavorable to June beetles seeking a suitable place for oviposition. As a result of a favorable plant environment, sods in these valleys are generally thick and are particularly dense. They contained less grubs than the adjoining slopes. Forty eight diggings gave 52,000 grubs per acre (Series 4) but on the adjacent thin hill-sides (Series 3) there were found 194,000 per acre from an average of 79 counts.

An examination of virgin and non-virgin blue grass sods revealed about the same relative infestations, respectively as were found in the other combinations although not quite so striking. A virgin blue grass sod (one which has never been plowed) is usually in excellent condition providing it has not been overgrazed. Counts in these sods (Series 5) showed 102,000 grubs per acre while 218,000 grubs were found in non-virgin pastures (Series 6) which had been cropped at one time or another and were not as fertile. Such sods had thinner turfs and grubs were more abundant. In some cases, virgin blue grass pastures had been excessively grazed in previous years, which gradually lowered the plant reserves until the sods became thin and the grubs more numerous.

The fourth combination of pasture conditions investigated relates to the use of sweet clover (*Melilotus alba*) seeded in permanent blue grass pastures. Graber⁵ has shown the value of sweet clover as a practical means for the improvement of blue grass pastures. Grub population determinations under these conditions were exceedingly indicative of crop selectivity by the adult beetles for egg laying. The highest average number of grubs found in any one field of sweet clover sown in blue grass pastures was 60,000 per acre, but most of the counts averaged around 28,000 per acre. The counts in the pastures immediately bordering the combination of sweet clover and blue grass showed 148,000 grubs to the acre from an average of 62 counts. A few of the clover fields had been seeded in 1928, the rest early in the spring of 1929. As the beetle flight occurred in May and June of 1929 the clover was present at the time of oviposition and was either in the seedling or second year stage of growth.

One of the most significant fields was in an old pasture considerably damaged by grubs in 1927 and 1928. A strip of sweet clover was planted in

⁴ See *Fig. 10, ECOLOGY, 12: 565.*

⁵ Graber, L. F. 1927. Improvement of permanent blue grass pastures with sweet clover. *Jour. Amer. Soc. Agron., 19:* (11), 994-1006. Illus. ——1928. Evidence and observations on establishing sweet clover in permanent blue grass pastures. *Jour. Amer. Soc. Agron., 20:* (11), 1197-1205.

this field in March, 1929 and the clover was several inches high when the beetles were ovipositing. Population counts were made in the sweet clover and adjoining blue grass during June, 1930. The sweet clover and blue grass combination contained approximately 20,000 grubs per acre and the blue grass 220,000 per acre.

SUMMARY

1. Population counts of white grubs in permanent blue grass pastures reveal that thick or very dense sods resulting from judicious grazing practices, ample fertility, and favorable moisture conditions are relatively free from grub infestations. Either the beetles have selective egg laying habits choosing the thinner sods of grass, weakened by an unfavorable environment, or with indiscriminate laying the eggs may fail to hatch or develop larvae capable of penetrating thick dense sods.

2. Grubs are much less numerous in thick stands of sweet clover established in permanent blue grass pastures than in adjoining pastures of blue grass growing alone. Such differences in grub densities are accounted for by an adult avoidance of sweet clover as a desirable crop medium for egg laying since it is assumed that if the eggs were laid in such places they would hatch and the grubs develop.

METHOD FOR DETERMINING THE DISSOLVED OXYGEN CONTENT OF THE MUD AT THE BOTTOM OF A POND

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During the course of a series of experiments on the respiration of certain mud-dwelling animals it seemed highly desirable that information concerning the amount of dissolved oxygen in the mud at the bottom of a body of water should be known. Accordingly an apparatus was designed by the use of which samples of water for oxygen determination could be collected from the mud. It is in the hope that the apparatus may prove useful to others that the following description is offered. The accompanying figure shows, in section, the essential parts.

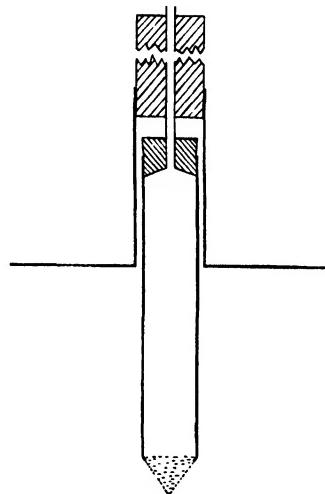


FIG. 1. Section of an apparatus used to collect samples of water from the mud at the bottom of a pond.

One end of a glass cylinder $1\frac{3}{4}$ inches in diameter and 10 inches long is heated and the diameter slightly reduced. To this is cemented (de Khotinsky's cement) a $1\frac{3}{4}$ inch alundum filter cone (RA 321.) in such a way that a water-tight union is obtained. The upper end is fitted with a perforated rubber stopper, into the lower surface of which has been carved a cone-shaped depression. A long glass tube, the length depending upon the depth of the water, is inserted into the stopper as indicated in the diagram. The tube is attached to a wooden rod for support.

When assembled and ready for use the cone is filled with paraffin oil, the stopper inserted and the lower end quickly let down through the water and

carefully but firmly pushed into the mud. The supporting rod is then anchored to a length of iron pipe which has previously been driven into the bottom.

In this position water from the surrounding mud slowly filters through the alundum cone and rises in the tube, due to the difference in air pressure in the tube and the pressure of the surrounding water. The paraffin oil, floating on the incoming water, seals it from contact with the air. The tube must, of course, be of sufficient length to extend well above the surface of the water. When the cylinder is filled and the level of the water in the tube approximates that of the surrounding water, a pressure equilibrium is established and the filtering process ceases. The whole apparatus is then detached from its anchor, raised to the surface, the stopper slowly withdrawn allowing the excess water in the tube to escape but leaving a layer of oil over the water in the cylinder when the stopper is completely removed. A sample of water can then be pipetted to the titrating bottle for determination of its oxygen content. The transfer of water to the titrating bottle is accomplished by the use of a large pipette the capacity of which is greater than that of the bottle. The pipette is filled by suction from beneath the layer of oil in the collecting cylinder. The water is then allowed to flow out gently into the titrating bottle (care being taken to avoid currents), until the bottle is full and the excess overflows. Repeated tests indicate that the amounts of oxygen absorbed by the water in this process are extremely minute.

The depth below the surface of the mud at which water may be collected is readily controlled by attaching to the sides of the wooden support the projecting arms from a large metal disc. The cylinder extends through an opening in the center of the disc. When the apparatus is being put into position, the disc, coming in contact with the surface of the mud, prevents further downward progress. By regulating the distance between the disc and the alundum cone, water can be collected from any desired depth of mud.

The apparatus, to be employed successfully, must have water-tight joints throughout. The union of the filter with the cylinder must be smaller than the diameter of the cylinder, otherwise water will be drawn down from above. Care must be used in setting the apparatus that the mud is not disturbed more than necessary, and after it is once placed it should not be moved about until the sample is to be collected. The alundum cone should be thoroughly dry at the time of placing in order that as small an amount of surface water as possible can pass through the filter while it is being quickly lowered in the water.

Metal cylinders can also be used, but the transparency of the glass was found to be a very desirable feature, especially when removing the sample.

The apparatus was used by the author to determine the amount of dissolved oxygen in the mud at two different parts of the same pond. The modified Winkler method of oxygen determination was employed. The following table indicates the findings.

TABLE I. *Dissolved oxygen content of samples of water filtered from various depths of mud*

Depth of water	Depth of filter in the mud	cc. of oxygen per l.	Time interval
Surface.....	—	4.33	—
8 feet.....	Surface of mud	2.36	2 hours
8 feet.....	4 inches	0.60	4 hours
8 feet.....	4 inches	0.75	5 hours
8 feet.....	10 inches	0.44	3 hours
8 feet.....	10 inches	0.35	19 hours
8 feet.....	12 inches	0.39	4 hours
8 feet.....	12 inches	0.38	18 hours
Surface.....	—	4.97	—
10 feet.....	Surface of mud	2.36	4 hours
10 feet.....	4 inches	0.13	4 hours
10 feet.....	4 inches	0.11	16 hours
10 feet.....	4 inches	0.10	19 hours
10 feet.....	4 inches	0.11	19 hours
10 feet.....	4 inches	0.14	80 hours

The oxygen content of the collected water remained quite constant regardless of the length of time elapsing between placing the apparatus and collecting the sample. If the sample either gained or lost oxygen the gain or loss should vary with the time; but even after eighty hours in the collecting tube approximately the same amount of oxygen was found as when the sample was taken only four hours after placing.

As was expected, relatively little oxygen was found in the mud. The respiratory processes of mud-dwelling organisms and the oxidation of organic materials in the mud constantly tend to deplete the oxygen. However, it is continually being renewed from the water above by agitation, either by currents along the bottom or by the activity of bottom forms.

Certain animal forms that live in tubes have access to the richer oxygen-bearing water above, but forms that do not construct such burrows but merely plow through the mud leaving no tunnel behind must get their dissolved oxygen supply from the water in the mud. Water extracted from the mud in the manner described above should yield fairly accurate information concerning the dissolved oxygen available to mud-dwelling organisms.

SUMMARY

An apparatus is described by which water can be collected from the mud at the bottom of a pond without excessive contamination by the water above. From the samples so collected the dissolved oxygen content can be determined which represents the amount of dissolved oxygen available to mud-dwelling forms. Experimental results obtained by using the apparatus indicate relatively minute amounts of dissolved oxygen in the mud. The amount of oxygen decreases with the depth at which the sample is taken.

Grateful acknowledgment is hereby made to the U. S. Bureau of Fisheries, whose laboratory at Woods Hole, Massachusetts was at my disposal during the conduction of these experiments.

WINTER HABITS AND YEARLY FOOD CONSUMPTION OF ADULT SPOTTED NEWTS, *TRITURUS VIRIDESCENS*¹

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Large numbers of spotted newts (*T. viridescens*) live in the small waters of eastern North America, and their habits are important to the aquatic societies of which they are members. Their consumption of insects and other organisms is large enough to be of significance in their communities. This is especially true in winter when they consume many insects, the survivors of summer broods, that are due to reproduce in spring and early summer. The activities of winter societies must greatly affect populations of the following summer. The following study of the winter habits and the food consumption of adult newts was made as a part of a more general study of the winter conditions in communities of water animals.

No special study of the food habits of *T. viridescens* is known to the authors except that of Matheson and Hinman (1929). No records of its winter food have been found, and but little note of its winter habits. The winter activity of newts (*T. viridescens*) on Long Island was mentioned by Noble (1926), who suggested that where plant life was rich the newts might not hibernate. He also suggested that in that region where many ponds dry up, the newts might hibernate on land, and gave November records of finding them hidden under logs.

Their methods of capturing their food were studied by Reese (1912), Copeland (1912), and Pope (1924). Matheson and Hinman (1929) recently showed the part which newts might take in controlling mosquitoes. They noted the scarcity of mosquitoes in pools where newts were abundant. Later they captured newts and fed them on a pure diet of mosquito larvae. The record of one such experiment was,—1100 mosquito larvae consumed by 3 newts in 8 days, or 45.8 larvae consumed per newt per day.

WINTER HABITS OF SPOTTED NEWTS

Adult spotted newts (*T. viridescens*) have been found semi-active and feeding all winter in ponds and spring-fed streams in Massachusetts. Among the newts examined, even those which were captured on the coldest days had recently-eaten food in their stomachs. This study was made upon newts of one spring-fed stream and a nearby pond in this region.

The stream was seldom frozen over even when the air was at below-zero temperature. Most of the mid-winter work was done in parts of it where

¹ This study was supported in part by a grant from the American Association for the Advancement of Science, and in part by a grant from the Sigma Xi Society.

the water flowed slowly over a mud and sand bottom two to three feet wide. In summer and fall, mats of Chara grew in the side-waters beneath its undercut banks or sometimes reached completely across its surface. Flat stones were scattered over a few places where the bottom was sandy. Collecting was carried on for nearly three years (June 1928–September 1931), newts being captured in every month of the year in numbers varying from 12 to 238 (Table I).

The fall migrations from land to water accounted for the increased number of newts in the stream during October and November. In those months they could be found often enough, peering out from the grass that bordered the stream, and skulking on its banks from which they eventually slipped down into the water. On warm October afternoons, a half dozen newts might be seen within a stretch of ten feet of stream-side. Throughout November they continued to go into the water; a few stragglers were seen creeping toward it even in December. Though of full size, these migrants were usually pale olive or yellowish green, distinctly lighter than the color characteristic of most of the breeding adults living in the same place during the spring season.

The newts spent the winter in the water in semi-hibernation. Through January they crept slowly about on the bottom even when the temperature of the air was but 5 or 10 degrees F. Throughout the winter months, they captured and ate other organisms (Fig. 1), and shed their skins with some frequency (Fig. 2). Although some of them were thus active, others were found crowded together in clusters of 20 to 40 beneath the flattened stones of the stream bottom. In the winter of 1929 similar clusters were found hanging partly dormant among the meshes of the half decayed Chara stems which filled the side-waters of the stream. Forty-six almost inert newts were taken from such a tangle of Chara stems on January 24, 1929. They could not have been inactive very long before they were collected for undigested food of recent consumption was found in the stomachs of nearly all of them.

FOOD CONSUMPTION OF ADULT SPOTTED NEWTS

In this study of their diet, the stomachs of 532 newts were examined. Usually the food had not been broken much and the organisms contained in it were easily recognizable. The bodies of soft midges were often in fragments but the heads were complete. The mollusk shells were only rarely dissolved thin by the digestive fluids. The posterior ends of the food masses were often different from the anterior ends, being discolored and more closely packed.

As already stated, the newts were collected through twelve different months during three years. The variation in the number collected and examined per month was very great, for example, 12 in August, 238 in July. Table I shows this variation giving the actual number of newts taken in each

month when collecting was done, together with the actual number of organisms that they had eaten.

Figure 1 shows the proportion of newts with and without food during a given month. In this figure the percentage of newts with food in each month is shown; in February only 20 per cent had taken food, while in September 100 per cent of them had eaten. In every month some newts were found

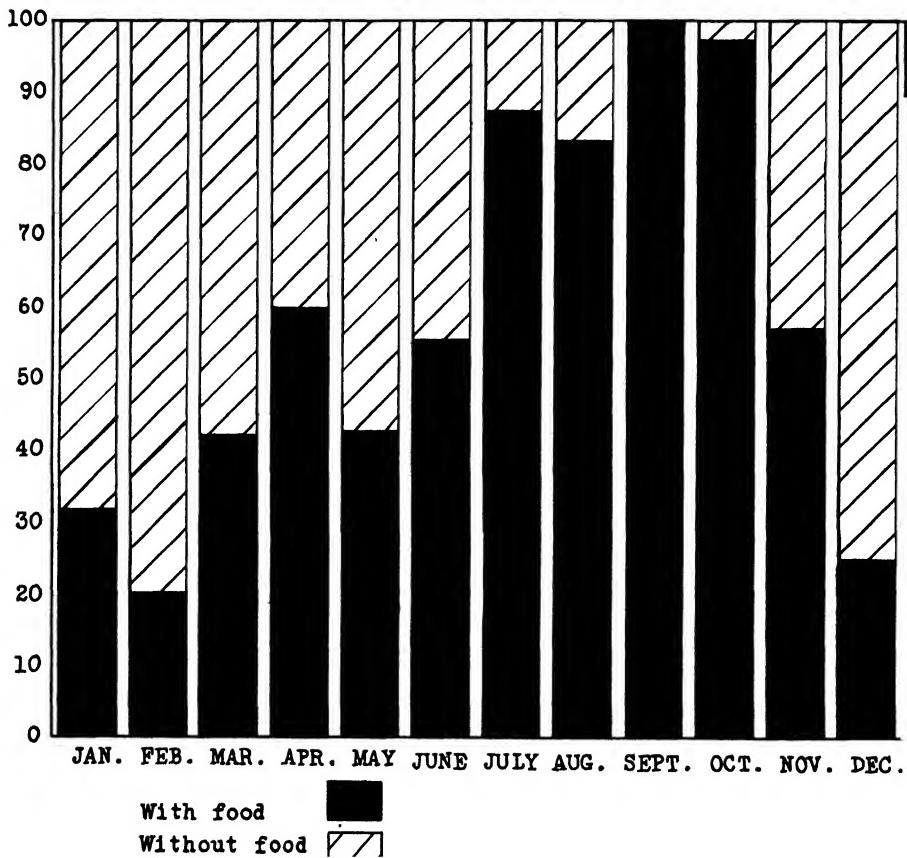


FIG. 1. Proportion of newts with and without food in twelve months of the year. Numbers indicate percentages of newts.

that contained molted skins; the percentage of these is shown in Figure 2. In January only fourteen per cent of them had eaten molted skins but in November there were 50 per cent with molted skins (Table II, Fig. 2).

Some of the newts studied were put into formalin as soon as they were caught, others two or three hours later, but none more than five hours after capture. The organisms and molted skins, taken from the stomachs were identified and counted but were not weighed. The graphs were also made on a numerical basis and hence only indirectly indicate bulk.

TABLE I. Food eaten by 373 adult spotted newts (*T. viridescens*) in 12 months. The numbers of newts with food varied greatly in different months

Date	Insects														
	Newts examined	Newts with food	Crustaceans	Mollusks	Amphibian larvae	Diptera	Odonata	Coleoptera	Hemiptera	Trichoptera	Ephemeroidea	Miscellaneous	Total insects	Molted skin	Skin but no other contents
January 11, '29.....	22	7				1					10		11	1	1
February 12, '29.....	20	4				3					1		4	1	1
March 10, '29.....	20	5				2					2		4	4	4
March 18, '31.....	6	6	2	1									18	1	1
April 7, '29.....	20	12				9					9		10	4	3
May 4, '29.....	20	7				2	1	1	1		2		4	2	3
May 18, '29.....	20	10	2				2	5	1		2		4	4	4
June 1, '29.....	20	11	15				2	5	2	1	1		9	2	2
June 12, '29.....	17	9	4	1		6	4	5	1	1	4		4	4	4
June 29, '29.....	15	9	25	2	2	1					2		20		
July 8, '28.....	8	4									3		7		
July 8, '30.....	230	205	801	5	8	367	7	142	23	5	66		613	63	1
August 8, '29.....	12	10	48			139	3	1	1	7	8		159	2	
September 24, '31.....	20	20	120	13	1	34	1	2	3	22	2		64	6	
October 27, '28.....	10	9	55			5				2	9		18	5	1
October 5, '29.....	24	24	13	38		9	7			5	7		75	9	
November 15, '28.....	16	9	11			2			3		8		14	4	
November 3, '30.....	6	4				4					1		4	3	4
November 10, '30.....	6	3	2			1					14		2	1	
December 14, '28.....	20	5	2								14		14	1	
Totals.....	532	373	1100	60	11	587	30	157	30	26	170	47	1058	109	15

TABLE II. A computation of the food eaten by 100 adult spotted newts (*T. viridescens*) per month based on data of Table I. Computation made in order to make food consumption of different months comparable and to secure larger numbers for the graphs (Figs. 3 and 4). The average number of organisms and molted skins actually consumed by one newt per month has been multiplied by 100.

Month	Newts with food	Crustaceans	Mollusks	Amphibian larvae	Diptera	Odonata	Coleoptera	Hemiptera	Trichoptera	Ephemeroidea	Miscellaneous	Total insects	Molted skin	Skin but no other contents
January.....	100			14.3						143.0		157.1	14.3	14.3
February.....	100			75.0						25.0		100.0	25.0	14.3
March.....	100	18.2	9.1		100.0		9.1			55.6	36.4	190.9	9.1	
April.....	100			11.8	11.8	11.8			8.3	75.0		83.3	33.3	24.9
May.....	100	11.8		27.6	34.5	24.1	3.4		17.2	11.8	47.1	35.4	23.6	
June.....	100	151.4	10.3	6.9	175.9	3.3	67.0	12.0	3.4	32.5	1.4	296.7	30.2	0.5
July.....	100	383.3	2.4	3.8	1390.0	30.0	10.0	10.0	70.0	80.0		1590.0	20.0	
August.....	100	480.0			1390.0	5.0	10.0		15.0	110.0	10.0	320.0	30.0	
September.....	100	600.0	65.0	5.0	170.0		21.2	6.1	21.2	48.5	112.9	281.8	42.4	3.1
October.....	100	206.1	115.1		42.4					56.3	280.0	125.0	50.0	25.0
November.....	100	81.3			43.8							280.0	20.0	
December.....	100	40.0												
Totals.....	1200	1972.1	201.9	15.7	2650.8	105.8	139.0	44.2	121.2	934.9	164.1	3585.6	316.5	105.7

In the analysis of the content of the food per individual in each month, obviously, only those individuals which contained food were considered. Molted skins were included as food (Fig. 1). The average number of organisms and molted skins eaten per newt in each month was then determined. For example, the total number of insects (11) eaten in January (Table I), was divided by the total number of newts which contained food (7), giving the average 1.57. In order to secure larger numbers for making graphs (Figs. 3 and 4), it was assumed that 100 newts contained food each month. The average number of organisms eaten per newt per month was then multiplied by 100. Since in January, 7 newts contained 11 insects (Table I), the

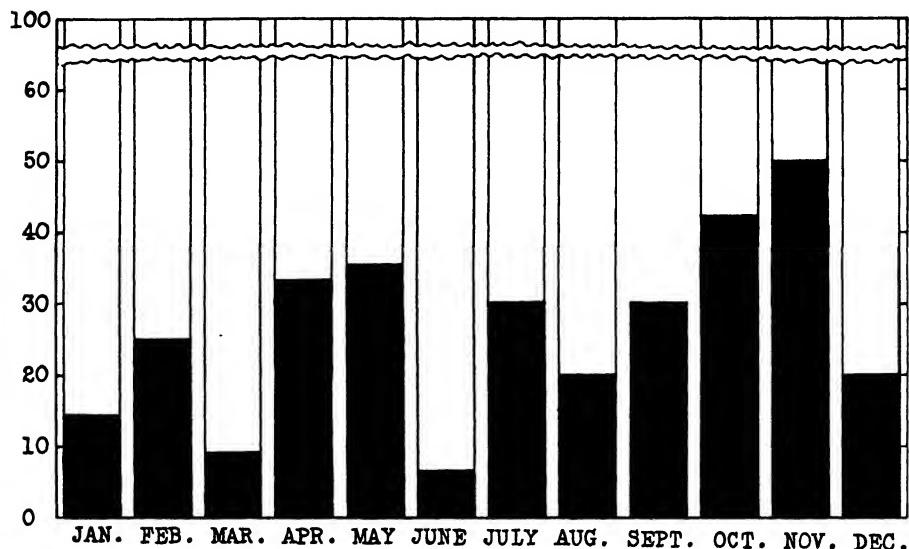


FIG. 2. Proportion of newts whose stomachs contained molted skins in 12 months of the year. Numbers indicate percentages of the newts containing skins.

assumed 100 newts contained 157.1 insects (Jan., Table II). In the year's total of 373 newts which contained food, there were 1058 insects (Table I). Thus, in the assumed 1200 newts there were 3585.6 insects (Table II).

The largest proportion of newts with food was found in September, 100 per cent (Fig. 1), the smallest proportion in February, 20 per cent (Fig. 1). Through spring the percentages of newts with food were low, March, 42 per cent (Fig. 1), and later they fluctuated around 50 per cent, but in July they began to rise, finally reaching their height in September and October (Fig. 1). There were fifteen newts whose stomachs contained nothing but molted skins, (Jan., 1; Feb., 1; Apr., 3; May, 4; July, 1; Oct., 1; Nov., 4.)

Molted skins were found in newts during every month. Evidently molting occurred frequently even in midwinter for in December, 20 per cent of the newts examined contained skin, in January, 14 per cent and in Febru-

ary, 25 per cent (Fig. 2). This and the winter food habits of the newts indicate an active metabolism going on the year round.

The organisms contained in the stomachs were identified to family or genus, and counted. Insects were eaten in every month, and from January through April they were practically the only food taken (Fig. 3). In 373

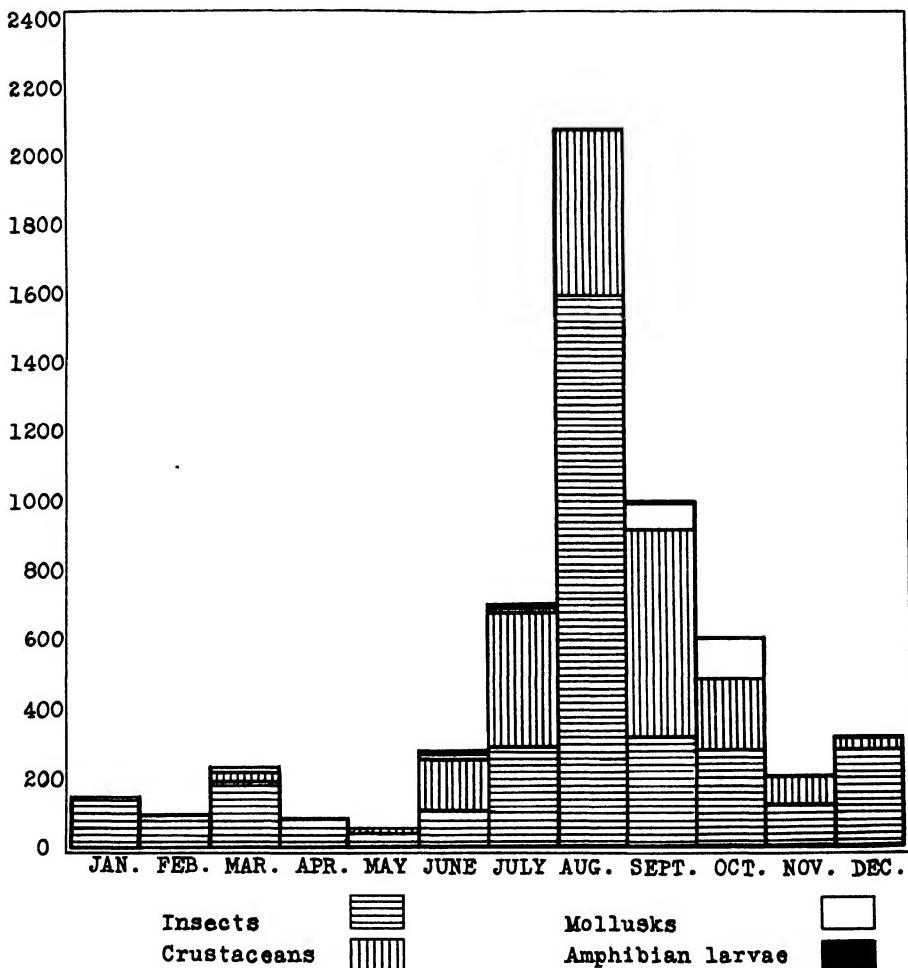


FIG. 3. Proportions of different groups of organisms represented in the food of adult spotted newts, *T. viridescens*. Numbers indicate numbers of organisms eaten (Table II) Graph shows the food of 100 newts based on computation from data in Tables I and II.

newts there were but 60 mollusks, mostly snails, (*Lymnea* and *Planorbis*), and a few clams (*Sphaeridae*) (Table I). This occurred in spite of the fact that mollusks were common in the water where the newts were caught. The occurrence of mollusks in the October diet may have been partly because in that month the newts were captured among thick growths of *Elodea* on

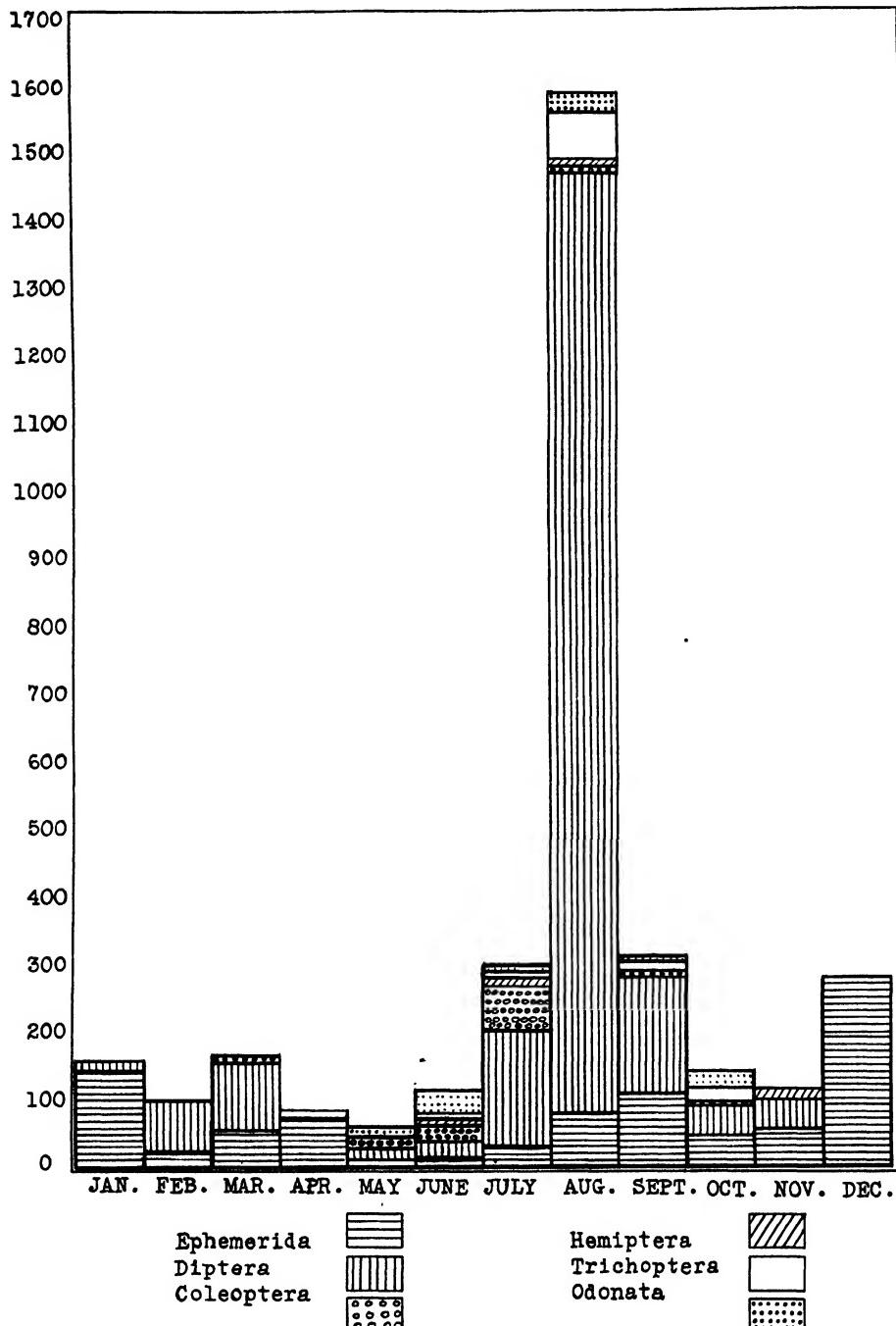


FIG. 4. Proportions of the different orders of insects represented in food of adult *T. viridescens*. Numbers indicate numbers of organisms eaten (Table II). Whole graph shows the food of 70 newts, based on computation from data in Tables I and II.

which the snails congregated in autumn. Of the actual total of 1100 crustaceans, 801 appeared in the July diet (Table I), although larger numbers per newt were eaten in August, September and October. One newt taken on August 8 contained 15 cladocerans together with 5 midge larvae and 3 pupae, 1 damselfly and 2 mayfly nymphs; another one caught on October 27 contained 8 cladocerans with their eggs, 4 ostracods and 2 copepods. The only amphibians contained in the food were 11 larvae of *T. viridescens* eaten in June, July, and September, although larvae of *Eurycea bilineata* as well as frog tadpoles were very common in the water. There were a few plant fragments probably swallowed with the animal organisms, and so small and so evidently accidental that they were not included in the graphs. Rarely, otherwise empty stomachs contained fragments of plant, probably eaten as a last resort. Typical records of such food are,—Dec. 12, Stomach almost empty, diatoms, filamentous algae, 10 fragments of higher plant; Oct. 29, Stomach nearly empty, 3 small pieces of leaf; May 4, 1 adult Dytiscus with filamentous algae on its legs.

The insects included in the food indicated to some extent the seasonal succession of insects in the populations amongst which the newts lived. There were midge larvae in it during 10 different months but only in small numbers until summer, when they steadily increased through July and into August. In that month one newt ate 50 midges. Mayfly nymphs were eaten in each month; they were the only food in December and the main one in January. The mayflies in the November food were Callibaetis, Siphlurus, and young Blasturus; in April there were 8 well-grown nymphs of Hexagenia. Few adult insects appeared in any of the food, chiefly tree-hoppers and aphids,—aerial insects which had fallen into the water (Tables I, II). Typical records of insect consumption were,—Aug. 8, 50 midge larvae, 1 stonefly nymph; Aug. 8, 1 dragonfly (*Anax*) nymph, 2 caddisfly (*Psilotreta*) larvae, 1 beetle (*Hydroporus*) larva; May 29, 10 aphids. In general the newts seem to have preferred soft-bodied, quick-moving insects. The newts examined throughout the year were uniformly carnivorous and when the bulk of food was considered, they were largely insectivorous. Their winter diet was made up almost solely of insects.

SUMMARY

In water, adult newts (*T. viridescens*) were found through the winter months often temporarily clustered together in groups of 20-40. The members of such groups were semi-active, easily disturbed, and often crept about over the bottom on mild days.

Adult newts were captured and the food content of their stomachs examined in every month of the year. Their food consisted of animal material, largely of insects.

The newts ate frequently all through the winter; they were found with recently eaten food in their stomachs even when the temperature was at zero

degrees F. Through December to May, their diet was almost purely of insects, largely mayfly nymphs.

They also shed their skins throughout the winter, since in newts collected in every one of the 12 months recently eaten skins were found in the stomachs. This indicated that very active metabolism went on through the entire winter.

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RECONSTRUCTION OF A LATE-PLEISTOCENE BIOTIC COMMUNITY IN MINNEAPOLIS, MINN.

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Our knowledge of the postglacial migrations of the flora and fauna of eastern America is still fragmentary and uncertain. It is based largely on inference from the present ranges and successional interrelations of species, direct fossil evidence being thus far extremely meager. Every find of post-glacial remains should therefore be utilized to the uttermost, as we have endeavored to do in the present case.

In the spring of 1923, during excavation for the new building of the Northwestern National Life Insurance Company, on Fifteenth Street opposite Loring Park in Minneapolis, abundant and well-preserved remains of plant and animal life of late Pleistocene age were discovered. A careful study of the locality and the deposits and an extensive collection of the organic materials have yielded the facts and conclusions presented in this paper.

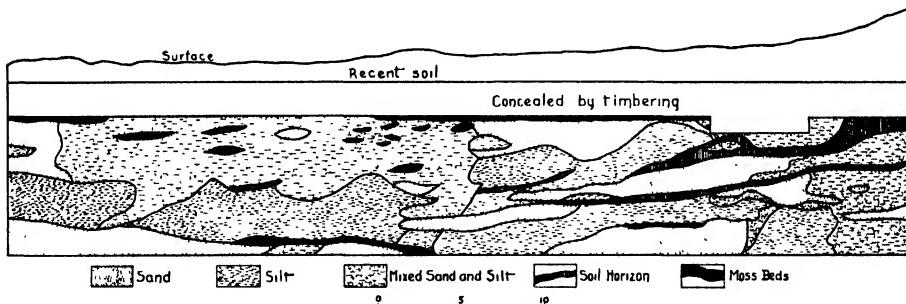


FIG. 1. Section in foundation trench, Northwestern National Life Insurance building Minneapolis.

The remains were disclosed in the walls of a trench prepared for the foundation of the building. The soil materials consisted of sands and silts in more or less lens-like masses, cross-bedded in part (Fig. 1). The maximum depth exposed was 12 feet below the local surface level. The upper portion of the natural soil was unfortunately concealed by timbering, the part visible above this interruption being the result of a recent artificial fill. At various levels were apparent soil horizons, and also beds of dominantly organic materials, principally mosses, which yielded most of the significant relics. The limited extent of most of the layers was indicated by imperfect corre-

spondence of exposures on the north and south walls of the trench, which was but five feet wide.

The general manner of deposition was evident. The sands and silts were dropped by flowing water which varied from time to time in velocity. The beds of aquatic vegetation denote periods when deposition by moving water was in abeyance. A glance at recent geological history will provide a logical setting for the events here chronicled.

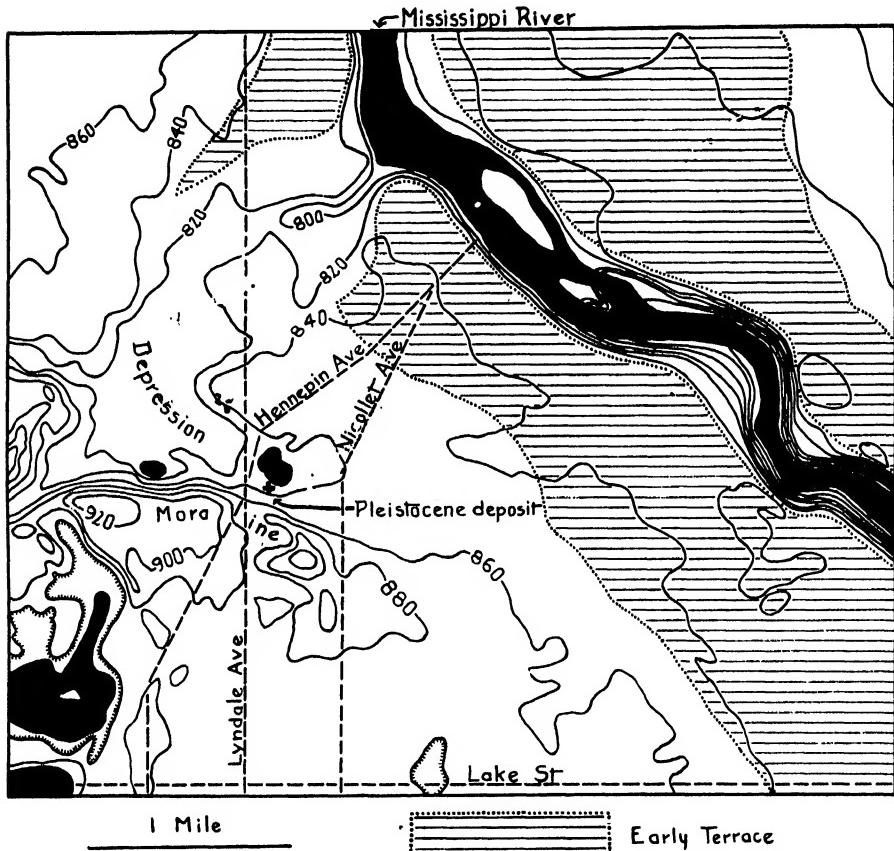


FIG. 2. A portion of Minneapolis and vicinity, showing late Pleistocene terrace and location of organic remains.

The Late Wisconsin ice sheet covered the region thinly, and after its disappearance from this vicinity the broad glacial Mississippi flowed nearby (Fig. 2). Sardeson ('16) designates the topographic result of the river's activity at this stage as the "Early Terrace," the altitude of which is here approximately 820 feet. Southwest of the strip of early terrace bordering the right bank of the river there lies at one point a shallow depression a mile and a half long and three quarters wide. Until metropolitan development

wrought drastic changes, it constituted a part of the valley of Bassett Creek, which throughout its course wanders from depression to depression in the random topography due to glacial deposition. This low area suggests a probable "backwater" of the Mississippi, in which stream-flow may have alternated with ponded conditions. The spot here considered would seem to be especially liable to such fluctuations, since its situation is not in the lowest part of the depression, but in an eastward extension of it where the surface is slightly above the 820 foot level of the early terrace. The lakelet in Loring Park, a few hundred feet north, is probably a remnant of the suggested backwater. Immediately south there is a high morainic ridge, a portion of which was cut away to make room for the new building.

In collecting the organic materials, samples were taken from various places on the two walls of the trench. These were numbered and their positions indicated on charts of the walls. A total of 83 samples was obtained. In segregating the various organic remains, blocks of the material were gently agitated in water to remove the silt. The mosses were carefully separated and spread upon paper towelling to dry. The shells of mollusca floated upon the surface and were removed with forceps or pipette. Fragments of *Chara* tubes and various miscellaneous objects were recovered in a similar way. In the case of samples containing much pollen, the surface of the water became covered with a film of grains.

The various sorts of organic remains were submitted to specialists for determination. Dr. R. S. Williams of the New York Botanical Garden took charge of the mosses and Dr. F. C. Baker of the University of Illinois identified the mollusca. The collections of the latter group have been deposited with the Museum of Natural History of the University of Illinois. The pollen was submitted to Dr. Paul B. Sears of the University of Oklahoma and the beetle wing covers to Dr. O. W. Oestlund of the University of Minnesota. Dr. F. K. Butters and Dr. C. O. Rosendahl of the University of Minnesota assisted in the determination of miscellaneous plant materials, some of which presented considerable difficulty. To all of these men we extend our sincere thanks. We wish also to express our appreciation of their assistance to the following persons: Dr. F. J. Alway of the University of Minnesota, who first informed us of the discovery of the remains; Mrs. Bertram D. Barclay and Mr. Raymond H. Landon, who assisted in the work of collection; and Dr. F. W. Sardeson of Minneapolis, who was consulted with regard to the physiographic situation.

In Table I we present a list of the organic remains obtained from the excavation. Two groups are at once apparent: the remains of organisms that lived in the pond, and the fragments that have been washed in from nearby terrestrial habitats. Among the first the mosses were by far the most abundant. Four species were found, all in considerable quantity. *Calliergon giganteum* (Schp.) Kindb., a living species, is an aquatic moss of northern range. *Drepanocladus fluitans submersus* Schp. is similar in range

TABLE I. *Organic remains from postglacial pond, Minneapolis, Minn.*

Animals		Plants	
Organisms	Evidence	Organisms	Evidence
Mollusca			
Amnicola gelida F. C. Baker (Ext.)			
Amnicola leightoni F. C. Baker (Ext.)			
Amnicola walkeri Pilsbry	Shells	Algae	Fragments of calcareous tubes; oospers
Amnicola walkeri precursor F. C. Baker (Ext.)		Chara sp.	
Fossaria obrussa decampi (Streng)			
Gyraulus altissimus (F. C. Baker) (Ext.)		Calliergon giganteum (Schp.) Kindb.	Plants
Gyraulus crista (L.)		Drepanocladus fluitans submersus Schp.	Plants
Gyraulus deflectus obliquus (DeKay)		Drepanocladus minnesotensis Williams (Ext.)	Plants
Helisoma antroса striata (F. C. Baker) (Ext.)		Neocalilegon integrifolium Williams (Ext.)	Plants
Helisoma campanulata (Say)		Abies sp.	Pollen
Lymnaea stagnalis jugularis (Say)		Picea glauca Voss	Cones
Physa sp.		Picea mariana B.S.P.	Cones, twigs (Seeds, pollen, wood of one or both species of Picea)
Pisidium sp.			
Valvata lewisi Currier			
Valvata tricarinata (Say)			
Ostracoda spp.			
Insecta			
Carabid beetle	Shells	Larix laricina K. Koch	Cone
		Pinus strobus L.	Pollen
	Wing-covers	Angiospermae	Fruits
		Potamogeton (filiformis?)	Spikelets
		Elymus sp.	Bark
		Betula papyrifera Marsh	

and habitat. *Drepanocladus minnesotensis* Williams, extinct, was here found for the first time (Williams, 30a). The fourth, *Neocalliergon integrifolium* Williams, also extinct, has been made by Dr. Williams the type species of a new genus. We may assume that the last two, being found intimately mingled with those still extant, were also aquatics. The two species of *Drepanocladus* were by far the most important, occurring in 89 per cent of the 32 samples containing moss remains, and forming the bulk of the material in most cases. *Neocalliergon* came next, both in frequency (46 per cent) and in bulk. *Calliergon* was comparatively neither abundant nor frequent (29 per cent).

Most of the moss material occurred in almost pure masses forming roughly horizontal beds. In Fig. 1 two principal strata are indicated, one at the top, partially concealed by timbering, the other near the bottom. Each was discontinuous in the sections, but the fragments may logically be united. The lower layer was represented also in the south wall of the trench; the area corresponding to the upper was not here visible. In addition to these main strata, several small lens-like masses occurred.

A complete vertical section of the lower moss layer was obtained at a point where it was 20 inches thick. The columnar mass, about 3 inches in diameter, was cut into segments 2 inches high, each of which was completely analyzed. Beginning at the bottom we find pure fine silt with no plant remains. Gradually, passing upward, a few scattered plants of *Drepanocladus* appear, small, slender, depauperate. From the second to the eighteenth inch the column appears superficially as a practically solid bed of mosses. In reality it is laminated, thin sheets of flattened moss alternating with thin beds of silt (Fig. 3, A, B, C). No part is entirely free from silt, even the moss layers being impregnated with it to some extent. The three mosses are distributed throughout the section, but definite zones of dominance of one or another are plainly marked, *Drepanocladus* and *Neocalliergon* being somewhat equally important, with *Calliergon* a poor third.

The history recorded in this bed is as follows. Sedimentation, which had been heavy for a time, gradually slackened and aquatic mosses began to grow, *Drepanocladus*, having a hard time of it at first, finally attaining dominance. Control passed from one to another of the mosses, until the renewal of active sedimentation put an end to their growth. The natural supposition would be that the mosses floated just below the surface of the pond, but Williams notes ('30) the occurrence of one of our species, *Drepanocladus fluitans submersus*, and also *Fontinalis antipyretica*, growing at a depth of 19 meters in a Wisconsin lake, the water of which is unusually clear. The water of our pond, however, must have been more or less turbid. We find preserved the broken fragments which sank to the bottom and were buried there. The small amount of silt between and with the moss layers came from the gradual settling of the "rock flour" borne by the glacial

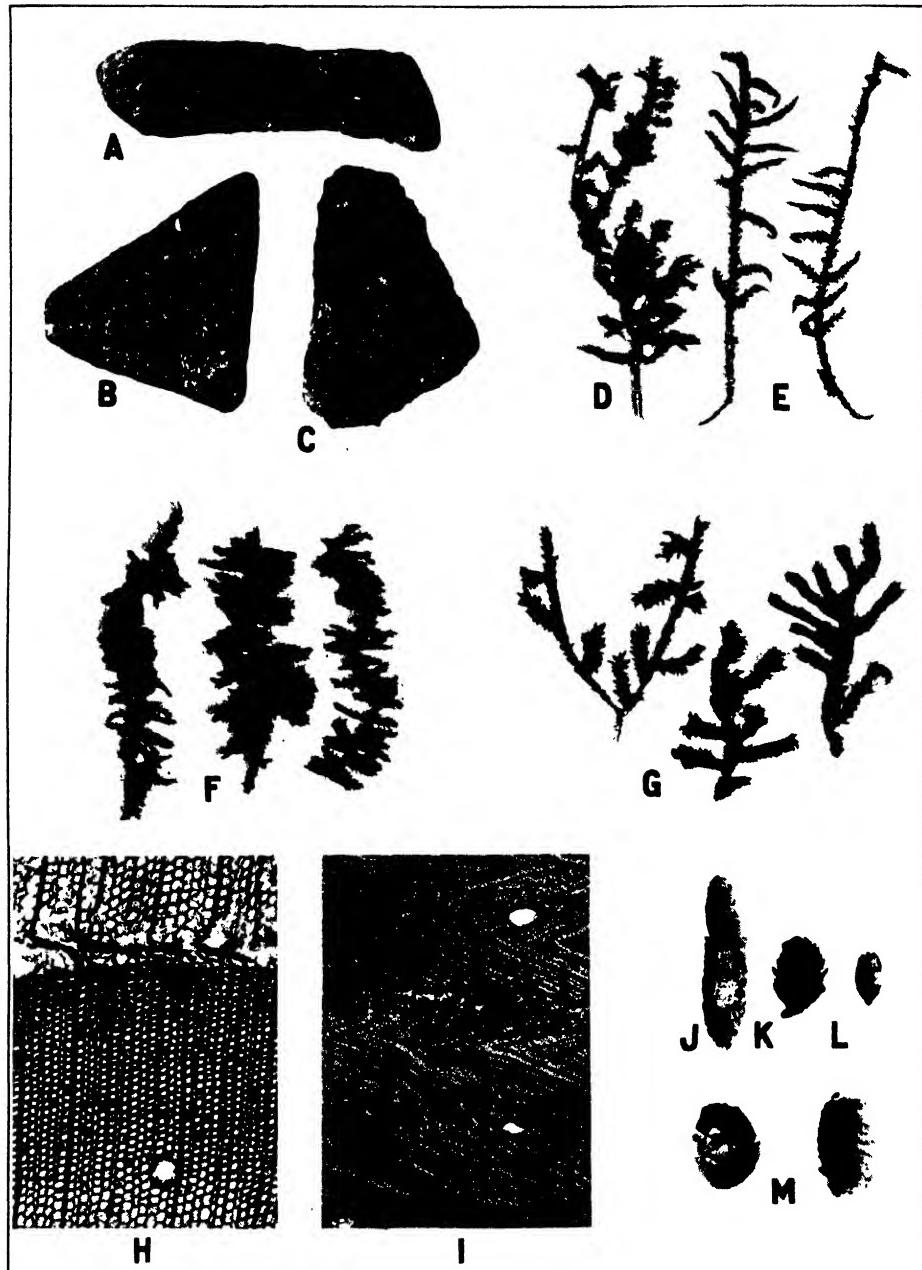


FIG. 3. Pleistocene plant remains found in the Minneapolis locality.

- A. Vertical section of moss-peat layer, showing alternating layers of moss and silt. Note mollusks in this and next.
B. Horizontal section of same through silty layer.
C. Similar section through moss layer; *Drepanocladus* and *Neocalliergon* visible.

waters. The lamination, with alternating layers of moss and silt, is conceivably annual—a sort of organic "varving."

Next in importance to the mosses in this section were the mollusca, which were found more or less abundantly throughout the column. Of the total of 15 species and varieties recovered from all samples, 11 were found here. Several of these have been reported by Baker ('11, '15, '20, '30) from postglacial deposits near Chicago, and, according to this author, the species still living are characteristic of quiet water two to ten feet in depth. The mollusca thus agree in habitat with the mosses. It was particularly noteworthy that in this section they were most abundant and in greatest variety at the bottom, where the mosses were practically absent. Ten of the 11 species were found in the lowest segment, whereas the other segments contained but three to five.

The upper moss layer and the scattered masses were essentially similar in character and contents to the one sectioned. A few additional remnants of pond life were found here and there. Casts and oosperms of *Chara* (Fig. 3, M) were recovered from four samples, one from near the top of the column just described. In two samples a few fruits of a *Potamogeton* were found, which seem like those of *P. filiformis*. A few ostracods were also discovered. These complete the known biota of the pond; all are in environmental agreement. Plotting the location of each find upon the vertical section fails to disclose any consistent differences between various levels. Evidently the pond filled slowly through intermittent sedimentation, in the intervals of which the same plants and animals repeatedly established themselves.

The remainder of the materials listed in Table I are structures of terrestrial origin washed or blown into the pond. Pollen was found in many samples, being particularly abundant in four. An analysis of the pollen content of these, made by Dr. Sears, is given in Table II.

Two communities are indicated by the pollen and other remains. One is the bog forest, proved by cones of tamarack (*Larix laricina* K. Koch) and cones, twigs and needles of black spruce (*Picea mariana* B.S.P.). The other is the climax forest, indicated by cones of white spruce (*Picea glauca* Voss), pollen of fir (*Abies*) and white pine (*Pinus strobus* L.) and bark of paper birch (*Betula papyrifera* Marsh). Wood of spruce of one or both species was scattered throughout the section, always in fragments. Sometimes

-
- D. *Drepanocladus fluitans submersus* Schp.
 - E. *Drepanocladus minnesotensis* Williams.
 - F. *Calliergon giganteum* (Schp.) Kindb.
 - G. *Neocalliergon integrifolium* Williams.
 - H. *Picea* sp.: wood structure almost perfect.
 - I. *Picea* sp.: wood much crushed.
 - J. *Picea glauca* Voss: cone.
 - K. *Picea mariana* B.S.P.: cone.
 - L. *Larix laricina* K. Koch: cone.
 - M. *Chara* sp.: oosperm, much magnified.

TABLE II. *Pollen analysis*

Sample	Abies	Picea (2 spp.)	<i>Pinus strobus</i>	Unknown	Pollen frequency
11	28%	60%	11%	1%	180
15	10	78	10	2	51
24	5	90	5		33
45	35	62	3		156

these were associated with the moss layers, but they were also found frequently in the sterile beds of silt and sand. In the majority of cases the cells were more or less crushed; in some they were in almost perfect condition (Fig. 3, H, I). All were recognizable as to genus by microscopic examination. Small fragments of charred wood were found at various depths in 13 scattered samples. Seeds of one of the spruces were in one sample.

Only two unimportant items are impossible to assign to their proper communities. Wing covers of a small carabid beetle were found in two samples, and badly frayed spikelets of a grass (*Elymus* sp.) in six. Wind may have carried the latter into the pond.

The foregoing analysis, fragmentary though it is, is adequate to permit reconstruction of the vegetation of the time. A morainic or outwash pond, sometimes flooded by silt-laden water, supported an intermittent vegetation of mosses, *Chara* and pondweeds, to which, if it were worth while, we might add an extensive group of probable companion species. Our list of mollusca gives a glimpse of the animal life. Nearby, in depressions of less depth, or possibly in sheltered re-entrants of this low area, grew communities of bog trees with their characteristic accompanying species. Upon the uplands, doubtless upon the very moraine that still rises just to the south, stood the climax forest of white spruce, balsam fir, white pine and birch, just as we find it today in northernmost Minnesota and upon Isle Royale (Cooper, '13). Branches, twigs, cones and seeds may have fallen from these trees directly into the water, and quantities of their pollen would inevitably reach the same destination. Forest fires are indicated by the fragments of charred wood.

During an expedition to southeastern Alaska in the summer of 1929 the senior author studied a locality that affords a remarkable parallel to the one in Minneapolis—a morainic pond in front of the Davidson Glacier, on the west side of Lynn Canal. In the half mile of distance between the present location of the receding ice front and the beach, one passes through the three normal stages of succession upon moraine: pioneers, willow-alder thicket and conifer forest. The pond in question lies near the outer margin of the morainic belt, and is surrounded by a dense forest of youthful Sitka spruce (*Picea sitchensis* Carr), in height seventy or eighty feet, with a maximum diameter of two feet. A few cottonwoods (*Populus trichocarpa* Hook.) are interspersed. An age count study upon a ridge adjacent to the pond yielded the following results:

Picea—73, 73, 72, 69, 60, 60, 63, 49 years

Populus—76, 71 years

From these ages and from knowledge of similar localities in southeastern Alaska we may conclude that the spot was uncovered by the melting of the ice one hundred to one hundred and fifty years ago.

The open water of the pond contained quantities of one of the same mosses found in the Minneapolis locality—*Calliergon giganteum*—also enormous amounts of *Chara* and two species of *Potamogeton*. In addition, another aquatic moss was present—*Fontinalis antipyretica gigantea* Sull.

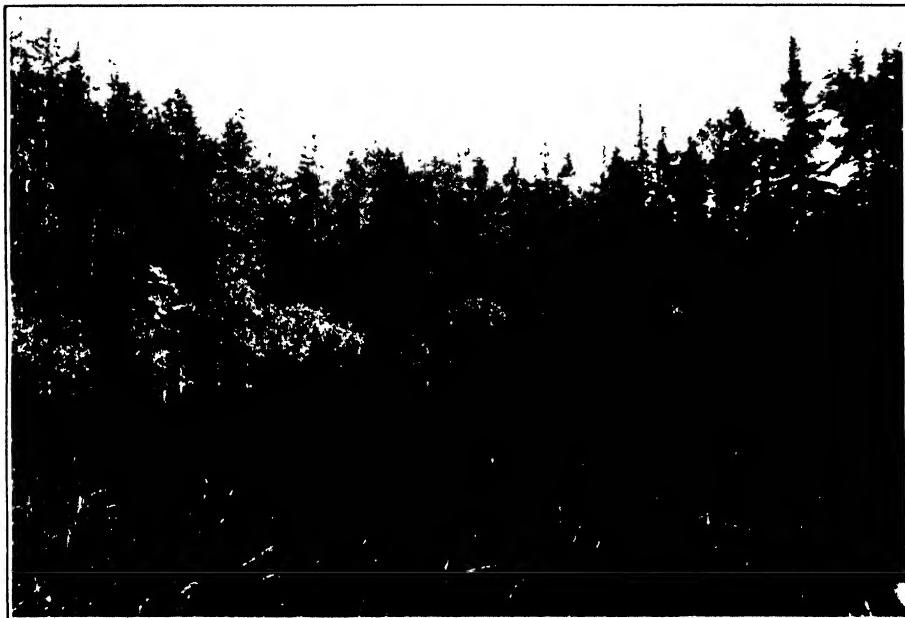


FIG. 4. Morainic pond in front of Davidson Glacier, southeastern Alaska.

Emergent aquatics filled the shallower portions, *Equisetum fluviatile* L. being most important. No collections of animal life were made.

A photograph of the Alaskan locality is presented here (Fig. 4). It is not difficult to imagine the conversion of such a pond into a deposit of "early postglacial fossil remains." Branches, cones and seeds of the spruces may fall directly into the water, and pollen is brought in by the wind. If, through change of course of an outlet stream, running water should invade the area, various materials from nearby communities would be deposited here and all buried under a layer of silt or sand. It is surprising that the species which most effectively resist the process of decay are such delicate plants as the mosses. This quality was strikingly shown in another Alaskan locality—Glacier Bay—where deposits related to a recent interglacial phase

yielded moss remains in which were found thirteen species in perfect state of preservation (Cooper, '23).

It is possible to set, with reasonable certainty, the period when the plants and animals lived, whose remains we have described. They flourished during late Pleistocene time, while the waning ice sheet still lingered within the present boundaries of the state, but before the initiation of Lake Agassiz. Physiographic evidence is rather conclusive on this point. Flowing water, with volume and velocity sufficient to lay down the silts and sands we have described, implies a connection with the Mississippi River. In order to inundate this locality, the Mississippi must have been flowing at least slightly above the 820-foot or "Early Terrace" level. During this stage, the river was a broad, heavily loaded stream, draining by many tributaries a wide expanse of ice front not more than 250 miles away. After the ice margin had receded over the divide into the lower country to the northwest—the basin of Lake Agassiz—the Mississippi lost its glacial load and most of its volume; it became transformed into a cutting stream, and immediately began to excavate an inner valley, thus preventing any further inundation of the locality under discussion.

The organic remains themselves testify to a great age, postglacially speaking. Some of the organisms, such as the tamarack and birch, exist in the immediate vicinity today, but distinctly as relicts. The black spruce still lingers in occasional bogs 25 miles north of Minneapolis. To find white spruce, except for an occasional group along the St. Croix River, one must travel northward a hundred miles. Although the bog forests still linger, the conifer forest which once inhabited the uplands, has been entirely superseded, here and for a hundred miles northward, by oaks, maples and other deciduous trees, and a great lapse of time is required for such a profound transformation. The best evidence of extreme age, however, is provided by the fact that five of the thirteen identified species and varieties of mollusca, and two of the four mosses, are extinct.

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THE INFLUENCE OF TWO BURROWING RODENTS, *DIPODOMYS SPECTABILIS* *SPECTABILIS* (KANGAROO RAT) AND *NEOTOMA ALBICULA ALBICULA* (PACK RAT)
ON DESERT SOILS IN ARIZONA

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INTRODUCTION

Although the importance of animals in soil formation is recognized, and is usually briefly mentioned in most soil text books under the title of "biological forces," little data has been presented to show just how important these forces might be. The literature contains a wealth of material concerning the activities of soil bacteria, fungi, protozoa, and to a much less degree, the invertebrate fauna of the soil. Little work, however, has been done concerning the constructive activities of various larger animals.

The relation of earth worms to soil fertility was first discussed by Darwin (1). The invertebrate fauna of the soil (Nematoda, Annelida, Myriapoda, Insecta, etc.) are discussed by Russell (4). Shaler (5) has given animals an important place in the soil formation, considering ants as playing a more active part than earthworms, and suggesting that vertebrates, especially mammals, have as great an effect as the lower forms of animal life. The activities of higher animals in this connection have been emphasized by Taylor and McGinnies (8), and by Taylor (7), who suggested that Shaw's formula for the expression of the principal factors controlling the trend of soil formation and development be modified to include the factor of animal life.

The purpose of this paper is to show quantitatively, from the results of chemical analyses, the effects produced in the soil by some of these higher animals. Two rodents, which are quite common in southern Arizona, the so-called banner-tailed kangaroo rat (*Dipodomys spectabilis spectabilis*) and the white throated wood rat ("pack" or "trade" rat) (*Neotoma albicula albicula*) will be considered. The life history of the former has been described in detail by Vorhies and Taylor (9), and a good description of the latter is given by Nelson (3).

The field studies were made on the Santa Rita Range Reserve, a grazing substation of the Southwestern Forest and Range Experiment Station, United States Forest Service. This substation is located at the northwest base of the Santa Rita mountains, approximately 35 miles south of Tucson.

EXPERIMENTAL METHODS

In the studies mentioned above, Reynard was interested in determining the burrowing habits of these animals, and also their effects upon the soil.

The burrows were carefully excavated, the tunnel system noted and drawn to scale on charts, and samples of soil were taken at various depths. These samples were composites, and in the case of the kangaroo rat were taken from several locations at each depth. The tunnel system of the wood rat is much simpler, since the tunnels are found at only a few levels. Other samples were taken 25 ft. distant from the burrow, and were designated as checks. The kangaroo rat, in digging its burrow, forms a mound; the height of which varies. Samples were also taken from it. They are designated as +4", +8", etc. according to the height above the ground level, while the others were labelled -4", -8", according to their depth below the ground level. The check samples were taken at the same depths as those from the burrow.

The soil samples were brought to the laboratory where they were dried, pulverized, and passed through a 2 mm. sieve. The methods used were those employed by the Department of Agricultural Chemistry, University of Arizona, for the routine analysis of soils and irrigation waters, and with a few exceptions were the same as those described by Hibbard (2).

A 1 : 5 water extract of the soils was obtained by shaking 100 grams of soil with 500 cc. of carbondioxide-free water for one hour in an "end-over-end" shaker. The extracts were then filtered under pressure through a Pasteur-Chamberland filter (Brigg's Design). The soluble salts present in the filtrate were determined.

RESULTS

Some of the results of the analyses are given in the tables below, expressed as parts per million present in the soil.

An examination of the tables reveals several interesting figures. In every case there has been an increase in the quantity of total soluble salts, due to the activities of these animals. Especially significant are the increases in soluble calcium, magnesium, bicarbonates and nitrates. In general, there was little variation in the quantities of sulphates, carbonates and chlorides. The increases in the latter are probably due to urination of the animals in the tunnels. This is especially the case of *Neotoma albicula* because the burrow system is not extensive; consequently there is a greater concentration of salts in a limited area. The increases in calcium and magnesium are due to the formation of bicarbonates and nitrates of these elements. This is supported by the fact that there is, with few exceptions, no marked increase in the amount of sodium, calculated from the differences between the sum of the negative ions and positive ions (calcium and magnesium) which were determined.

Most of the soils of Southern Arizona are calcareous, and contain quantities of calcium carbonate varying from one to twenty or thirty percent. Any increase in acid ions would be immediately neutralized by the calcium carbonates.

The unusual increase in the quantity of nitrates is due to two factors:

the excreta of the animals and the material which both of these animals carry to their burrows. Both defecate promiscuously in these tunnels, and the wood rat also collects a wide variety of articles other than food, which consist principally of plant material. Investigations by Dr. P. S. Burgess and R. A. Greene have demonstrated that the soils of Arizona have a very active microbiological flora—especially those groups of organisms responsible for nitrogen fixation, nitrification, and cellulose decomposition. Consequently, any organic-nitrogen-containing substance would be rapidly decomposed and converted in a large part to soluble nitrates, which in turn would be converted to calcium nitrate.

The carbon dioxide produced by the respiration of these animals is probably responsible for the increase in the quantity of bicarbonates. In the presence of moisture (from the soil or other sources), carbonic acid is formed. This has a pronounced solvent action upon calcium carbonate, and as a result calcium bicarbonate, which is much more soluble, is formed—a process identical with the formation of caves in limestone areas. The idea is further supported by the fact that, from the analyses, the authors were generally able to identify the zone of greater activity which was evidenced chemically by an increase in soluble calcium, magnesium, and bicarbonates. This was especially so in the case of the kangaroo rat which has a complicated system of tunnels at different levels. Charts of the burrows, which were prepared by Reynard, showed that the greatest salt concentration was found at the levels of greatest tunnelling. For example, compare samples number 17071 and 17005 (Table I): 17174, 17177, 17168 and 17171 (Table II).

In each case there is a considerable increase in the quantity of nitrates. The effects of these increases may sometimes be observed riding over the Santa Rita Range Reserve. The vegetation in the environs of a deserted burrow, which has weathered somewhat, often has a more luxuriant growth and the typical deep green, "healthy" color of plants well supplied with nitrates, while the more distant plants lack these features.

DISCUSSION

It is appropriate to include a discussion of the significance of the activities of these animals. While the analyses given above are by no means all-inclusive, they do represent the major soluble constituents of the soil. There are no chemical means for determining the fertility value, or the needs of a soil. Certain biological methods, such as the Azotobacter or plaque method for estimating the availability of phosphorus, which has been highly recommended in certain sections, apparently has slight value in Arizona. For lack of a better method, however, the soluble salt determination has been used for years in the western states, especially in California, Utah and Arizona, as a means of determining a few limiting factors of plant growth. An examination of the tables shows that in very few cases do the total soluble

TABLE I. *Kangaroo rat burrow no. 1*

Lab. no.	Description	Total soluble salts	Sodium	Calcium	Magnesium	Chlorides	Sulphates	Carbonates	Bicarbonates	Nitrates
17002-70	Top of burrow (check-surface).....	537 182	72 35	75 0	30 15	110 50	0 trace	0 0	48 36	200 45
17003	+6"	66	30	15	22	70	none	0 0	61 61	200 200
17004	Ground level (burrow)	449	52	15	15	50	0	0 0	98 98	75 75
17005-71	-6"	305	93 35	150 0	0 0	60 40	trace	0 0	158 40	450 20
17006-72	-12"	912 159	62 22	30 0	15 15	40 40	trace	0 0	85 48	180 0

TABLE II. *Kangaroo rat burrow no. 3*

Lab. no.	Description	Total soluble salts	Sodium	Calcium	Magnesium	Chlorides	Sulphates	Carbonates	Bicarbonates	Nitrates
17172-68	Top of burrow (surface check).....	56 22	120 30	0 0	70 50	0 0	0 0	0 0	195 49	200 15
17173	+8"	216	225	22	120	0	0 0	0 0	171 171	450 450
17174	Ground level (burrow)	1204	—	500	37	170	0 0	0 0	146 146	1000 1000
17175-69	-6"	1853	25 28	180 45	45 0	130 70	0 0	0 0	171 85	450 10
17176-70	-10"	1001	238	135 30	30 7	80 70	trace 0	0 0	171 98	340 10
17177-71	-24"	938 253	360 30	30 7	160 80	0 0	0 0	0 0	366 98	800 12
		1905 279	212 59							

Figures in italics give the results of check samples which were taken at a distance of 25 feet from the den.

TABLE III. "Wood rat" burrow

Lab. no.	Description	Total soluble salts	Sodium	Calcium	Magnesium	Chlorides	Sulphates	Carbonates	Bicarbonates	Nitrates									
18467-76	Excav. 1, burrow, -4' (check, -4').	1769	196	98	29	225	15	112	7	210	20	0	0	24	0	610	110	490	15
18469-68	Excav. 2, burrow, -10' (check, -10').	4621	226	604	0	450	15	180	30	420	20	800	0	36	0	1171	146	900	15

TABLE IV. "Wood rat" burrow

Lab. no.	Description	Total soluble salts	Sodium	Calcium	Magnesium	Chlorides	Sulphates	Carbonates	Bicarbonates	Nitrates								
18536-35	Nest 3, burrow (check, -12') -12'.	833	157	trace	150	15	67	22	20	0	0	0	0	476	85	120	15	
18538-37	Same, burrow -16' (check -16').	845	157	trace	20	225	15	97	7	50	30	0	0	0	293	85	180	trace

Figures in italics give the results of check samples which were taken at a distance of 25 feet from the den.

salts present exceed the toxic limit for sensitive plants, such as citrus (about 1000 ppm. of soluble salts, the sodium chloride content of which should not exceed 500 ppm.). Furthermore, the salts present are chiefly salts of calcium and magnesium, which are not as toxic as those of sodium. With a few exceptions (especially No. 18469, Table III) the total salt content is not great enough to be injurious to any field crop common to Arizona.

For the most part, the quantity of nitrates present would be injurious to plants. These, however, would be removed to a great extent by leaching and subsequent absorption by plants.

Another important effect brought about in the soil by these animals is aeration and increased water percolation, due to burrowing, as well as a considerable increase in organic content, from the plants and other materials (dung, etc.) carried into these burrows.

A still more important result is the effect these animals have upon the availability of phosphorus. These soils of the arid section are characterized by a deficiency in nitrogen, small quantities of available phosphorus, and an abundance of available potassium. The few fertilizer experiments which have been conducted by the Arizona Agricultural Experiment Station have often shown a response to phosphorus fertilization. Further studies have demonstrated it not to be a deficiency in total phosphorus present in the soil, but to a deficiency in available phosphorus. It has been noted that these soils studied are all calcareous, and all have a pH value well above neutrality; these pH values vary from approximately 7.5 to 8.4, the average being somewhere near pH 7.8. Under such conditions, soluble phosphates are rapidly "reverted" to an insoluble form, chiefly tri-calcium phosphate ($\text{Ca}_3(\text{PO}_4)_2$). Recent work of J. F. Breazeale and W. T. McGeorge in this laboratory has demonstrated that carbon dioxide is closely connected with the availability of phosphorus in the soil. It does not seem unreasonable to assume that the carbon dioxide produced by respiration of these animals may have a similar influence upon the soils.

The deficiency of nitrogen in these soils has also been mentioned. An average desert soil will probably not contain more than 0.015 to 0.022 per cent of total nitrogen, and a correspondingly small amount of soluble nitrates (0-15 ppm.). Consequently, there is a decided response to applications of nitrogen. The amounts of soluble nitrates found in these soils, resulting from the biological activity of these animals, is rather large (0.1 per cent of NO_3 in sample 17174).

The economic significance of these animals may be realized more fully by giving a few examples. There is generally only one animal per burrow, which may cover an area of 5 to 15 ft. in diameter, and may have a depth of several feet. The dimensions of the kangaroo rat burrow No. 1 were 8 by 10 ft., and the maximum depth was 16 inches. The total volume of the den was 110 cubic feet. Burrow No. 3 was slightly larger (volume 120 cu. ft.). The average nitrate content of the former was 221 parts per million, and 570

ppm. for the latter. Assuming the volume weight of the soil to be 1.5, burrow No. 1 would contain 3.65 pounds of nitrates (NO_3) or 0.83 pound of nitrogen, and burrow No. 3 would contain 10.26 pounds of nitrates or 2.32 pounds of nitrogen. At the present market price, the nitrogen present in these burrows would have values of 16.6 and 46.4 cents respectively. Taylor (6) estimates the rodent population of the Santa Rita Range Reserve at 2,000,000, of which about 500,000 are wood rats and 100,000 are kangaroo rats. If the average nitrogen value of the kangaroo rat burrow is assumed to be 31.5 cents, the total value would be \$31,500. The area of the wood rat burrows is much smaller than that of the kangaroo rat, but, assuming the value of nitrogen in each wood rat burrow to be 10 cents, the value would be \$50,000, or a total of \$81,500, which could be attributed to the activities of these two animals. This does not include the quantity of food stored by these animals, which Taylor estimates at 400,000 pounds per year for the kangaroo rats alone. The excavations of the burrows showed that only a small proportion of material is stored in excess of maintenance needs. The actual residue is probably only about one fifth (or less) of the figure given above. Even so, the quantities of organic materials carried into the burrows by these two animals would be significant.

Only the preponderantly beneficial effects of these animals have been discussed in the preceding paragraphs. It is very difficult to form any opinion as to whether, in the final analysis, these animals are economically beneficial or detrimental. Although there is little experimental work to support the idea, it is improbable that the numbers of kangaroo rats are limited by food supply alone. Where grazing range is conservatively handled, there is an excess of forage above all needs for livestock or for protection of watershed, except in abnormally dry seasons. Consequently, the consumption of forage by these animals is probably of little economic importance except on overgrazed ranges or in extremely dry seasons. A part of this forage is stored by the animals in their burrows, and a small part of the food consumed is returned to the soil in the excreta of the animals. Both of these factors add to the fertility of the soil, and in addition, there are also the physical effects produced by the burrowing of the animals and the probable increase of phosphorus available for plant use. Under present conditions, except where the local situation becomes acute, it will probably be best to await the results of further studies before instituting any widespread control campaign. Until such studies are made, the economic status of these animals cannot be verified, although it does not seem impossible that the beneficial effects may, at least, be equal to the injurious effects.

SUMMARY

Representative soil samples have been secured from the dens of kangaroo rat (*Dipodomys spectabilis spectabilis*) and the wood rat (*Neotoma albicula*

albibula). Similar samples have been secured from the unworked soil in the vicinity of the dens.

These samples have been analyzed, and those from the dens compared to those which had not been subjected to the influence of the animals.

In every case the soil from the dens contained a larger quantity of soluble salts. These increases were especially pronounced in the case of calcium, magnesium, bicarbonate, and nitrate ions.

The relation of these animals to soil fertility has been discussed and the conclusions are that, in the long run, the beneficial effects would overshadow the ill effects, and that these animals are exerting measurable influences upon the chemical and physical properties of the soil.

The relation of the amount of vegetation consumed by these animals to the increase they cause through increased soil fertility has not been determined. It is probable that their consumption of forage is of little economic importance except on overgrazed ranges and in dry seasons.

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SALINITY OF THE MEDIUM AND ITS EFFECT ON RESPIRATION IN THE SEA-ANEMONE *

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The effects of pure salts and increase of salinity of the medium on marine cells and organisms, with respect to respiratory activity and metabolism, have been reported by a number of observers. (Warburg, 1908; Meyerhof, 1911; Page, 1929; Chambers and Reznikoff, 1925; Gustafsen, 1921; Hess, 1930; Brooks, 1919.) However, the sea-anemone, *Metridium marginatum*, has not been studied by the most accurate methods. These animals, exposed to currents of sea-water of varying salt-content, or when at the mouths of rivers quite often brought into contact with fresh and brackish waters, should exhibit some response to such a changing environment.

Bodine (1928) has pointed out that KCl is toxic for the larvae, embryos and eggs of Fundulus, and that NaCl and CaCl₂ are also quite toxic, with mixtures of K and Ca ions showing some antagonistic ion action causing them to be less toxic for the eggs, but quite toxic for the larvae and embryos. Pantin (1931) and Pantin and Weil (1931) have shown the reactions and adaptations for a flatworm to fresh, brackish and sea-waters. In most of the organisms studied, it is indicated that an increase in the NaCl content causes an increase in the metabolism as measured by oxygen uptake, while the addition of KCl will also cause increased metabolism. The addition of CaCl₂ to the medium usually causes a return to the normal respiratory rates, indicating an antagonistic ion effect. Increase in the salinity of the medium would be expected to bring a rise in metabolic rate, even though possibly only a temporary one, probably due to the toxic effect of increased salinity and osmotic pressure.

A number of experiments were conducted with small specimens of Metridium in the respiratory chamber of the Thunberg-Winterstein microrespirometer (Thunberg, 1905; Fenn, 1927), the animal being allowed to remain in the apparatus while experimental runs were made with the natural sea-water as the immersion medium, with dilute or concentrated sea-waters of known salinity (Page, 1928; McCallum, 1926), or with the sea-water replaced by solutions of pure salts. A large number of experiments could be run on the same organism, the animal being allowed to settle down and fasten itself to the bottom of the respirometer chamber and live there, and at the conclusion of a series of experiments the unnatural medium was replaced by sea-water allowed to run continuously over the organism.

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In each of a series of experiments the normal respiration of the organism was taken in natural sea-water before being washed and covered with the abnormal medium. Hence, one always had an accurate check on the normal respiration before subjecting the animal to experimental conditions, as well as a check on the ability of the animal to recover its normal metabolism.

Figure 1 shows the type of respirometer chamber in the apparatus used in all the experiments. The small cup in the center of the chamber contains KOH to absorb carbon dioxide as fast as formed, a decrease in the volume of gas in the respiration chamber due to usage of oxygen producing a negative



FIG. 1. Type of respirometer chamber used in experiments.

pressure drawing a drop of kerosene through the capillary between the two chambers of the instrument in proportion to the amount of oxygen used. Figure 2 illustrates data of two experiments with a small Metridium of 150 milligrams weight, showing (Experiment 24) normal respiration in normal sea-water of a salinity of 30 parts per 1000, and, the rate of respiration in a hypertonic sea-water of 45 parts per 1000, corresponding to 150 per cent sea-water. A third curve shows a further fall in respiration rate when the organism was exposed to concentrated sea-water of 60 parts per 1000, or 200 per cent sea-water. Experiment 30 illustrates the typical results with the same individual organism after complete recovery and when changed to media of hypotonic sea-water of 15 parts per 1000 and 10 parts per 1000 of total salts. It will be noted there is again a corresponding reduction in the metabolic rate as measured by respiration rate when in the unfavorable environment. In every case, when the medium varied from the optimum of 30

parts per 1000 in salt-content there was a decrease in the respiration rate and not an increase, as one might be led to expect from experiments on other organisms.

It is interesting to note also that when the sea-anemone was immersed in either M/4 or M/2 NaCl, in M/4 or M/2 KCl or in M/4 or M/2 CaCl₂ instead of the natural medium, the only observable result on the respirometer reading was a pronounced decrease in the rate of oxygen consumption, again following an unfavorable change in the medium surrounding the animal.

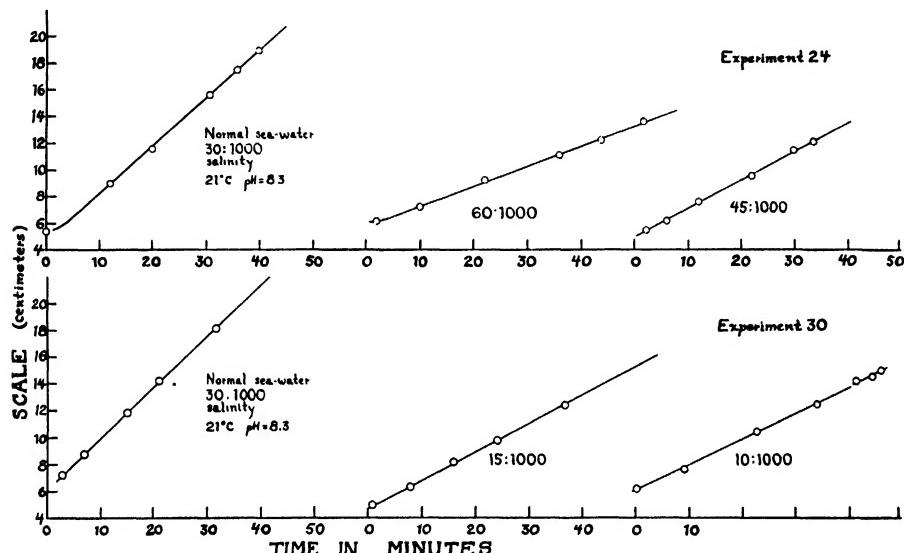


FIG. 2. Results of two experiments on rate of oxygen consumption at different saline concentrations.

Figure 3 shows the sort of curve that results when one attempts to plot percent of respiration (based on respiration in a 30/1000 medium as 100 per cent) against the salinity of the medium. It will be noted here also that the further away from the optimum salt concentration of the sea-water, the greater is the decrease in the respiratory rate.

An interesting change in the extension of the animal always accompanies any marked change in the rate of respiration when in an unfavorable medium. In all hypotonic solutions the animal remained extended until the salinity had decreased to about one-third of the normal value, *i.e.*, to 10 parts per 1000 or 33-1/3 per cent sea-water. In all such cases the organism had contracted to one-third or one-fourth its normal length and had slightly withdrawn the tentacles. However, when the organism was brought into contact with hypertonic sea-water a marked contraction of the whole organism occurred depending on the degree of hypertonicity of the medium, until in a saline concentration of 200 per cent sea-water (60 parts per 1000) every specimen of Metridium contracted completely to a flat plate

of tissue, and had withdrawn the tentacles completely, at the same time secreting a mucous covering over the entire organism. In all such cases nematocysts on the body were discharged. Even after exposure for a period of two hours to a very concentrated saline solution (200 per cent sea-water), the specimens of *Metridium* always recovered in about four hours and regained their normal respiratory rate, normal activity and extension in the sea-water circulating in the laboratory.

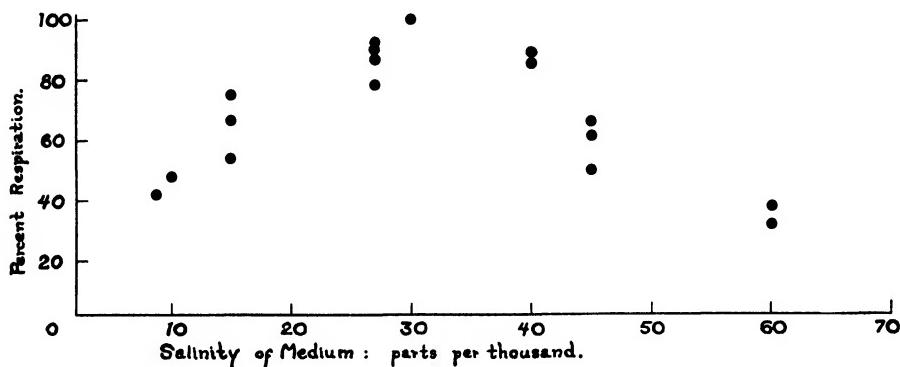


FIG. 3. Experimental data on the effect of salinity of the medium on per cent of normal respiration.

Metridium marginatum is capable of regulating its distension and surface of contact quite readily in various saline solutions. The oxygen consumption seems mainly a matter of the degree of extension of the organism, and this depends to a large extent on the optimum oxygen concentration, salinity, and osmotic pressure conditions in the medium. Oxygen consumption appears to be mainly a matter of diffusion into and through the tissues of the organism, and a protecting device against an unfavorable medium, such as the secretion of mucous, greatly slows the respiratory rate by preventing the diffusion of oxygen into the tissues. It is for this reason that the sea-anemone is extremely variable and ill-adapted material for respiration studies. One is unable to cause the animal to remain in the same position of extension under a series of varying experimental circumstances.

SUMMARY

1. *Metridium marginatum* has been studied with reference to changing rates of respiratory activity in different saline concentrations of the medium.
2. Any variation of saline concentration from ordinary sea-water causes a decrease in respiratory activity accompanied by contractions of the body.
3. Pure salts of Na, Ca, and K, cause a pronounced decrease in the respiratory rate and an increased contraction of the organism.
4. Because of continuous changes in extension and activity this organism is ill-adapted to studies on respiratory activity under experimental conditions.

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REVIEWS

WICKEN FEN

The "Fenland" of the east of England represents one of the conspicuous landscape types that has remained relatively unchanged throughout historic times. It occupies a great plain of over a thousand square miles, which is really a complex delta of a group of rivers emptying into "The Wash." This great bay has been gradually filling up during post-glacial times with deposits of peat and silt. The former deposits are best developed in the south around the tributaries of the River Ouse. In this area one of the spots which has escaped, to a large extent, changes due to drainage is Wicken Fen, first brought to the attention of ecologists through the investigations of Yapp.¹

Wicken Sedge Fen forms an area of some 400 acres and while ditches and other "lodes" intersect it in various directions, it is still practically un-drained, only the surplus rain water finding its way by means of Reach Lode into the River Cam, a tributary of the Ouse. The Fen is surrounded by relatively dry lands and is probably very gradually becoming drier, although very slight changes have been recorded since its vegetation has attracted the attention of the ecologists of Cambridge University.

Its vegetation² comprises types of rather unique interest both to the fenmen, who distinguish "sedge," "litter," and "carr" and to ecologists, who recognize various marsh associations.

The "sedge" consists almost wholly of *Cladium mariscus*, a slow-growing evergreen plant which forms, if left to itself, very dense growths, often to the exclusion of other species. For decades and probably for centuries considerable areas of it have been cut over about once in four years and the crop used for thatching. Where cutting has not occurred there is formed from the wiry tough leaves a "dead leaf mattress" which may attain to a thickness of two feet, and which tends to insure the "sedge" from the possibility of invasion by any other species. "Litter," on the other hand, is a more mixed community dominated by *Molinia coerulea*. It is usually cut each year and the crop used for bedding cattle or occasionally for feeding. The "carr" is a shrub community in which the chief species are *Rhamnus frangula*, *R. cathartica*, *Salix cinerea* and *Viburnum opulus*.

The agricultural treatment of the fen in addition to the cutting of litter and sedge includes the making and upkeep of "droves" or walks which have

¹ Yapp, R. H. Sketches of vegetation at home and abroad. IV. Wicken Fen. *New Phytol.*, 7: 61-81. 18 figs. 1908.]

² Godwin, H. and A. G. Tansley. The vegetation of Wicken Fen: The natural history of Wicken Fen. Pt. 5, 387-446. Figs. I-II. 1928. *Bowes and Bowes, Cambridge.* 3s. 6d.

their own characteristic vegetation, the periodic clearing of bushes and the cutting and clearing of ditches. Peat has also been cut from time to time in some parts of the fen. All these activities serve to increase the complexity of the plant cover of the fen and to make more difficult the understanding of the ecological relationship of the various types of vegetation.

In attempting to explain this confusing mixture of plant communities, Godwin³ concludes that the checkered fen vegetation is caused by the presence of all stages of primary succession, of various stages of two deflected successions produced by heavy and light cutting respectively, and in addition, various true secondary successional stages produced by the recolonization of land cleared by the digging up of the bushes in mature carr.

Thus Wicken Fen is not only ecologically interesting because it is a relict of undisturbed primitive fen, but also because it is a relict of the old English fenland which displays the reaction of plant communities to different aspects of a very ancient mode of agriculture.

Godwin and Tansley have given a close analysis of the plant communities and have traced the succession from open water through various aquatic communities to reed swamp, "sedge," "litter," and "fen carr" to a mature carr which seems to be the forerunner of a deciduous forest. They have recorded differences of vegetation that seem to have arisen from differences in the cutting, draining and other manipulation of parts of the area. Still more important, they have instituted a series of records, including permanent quadrats, which promise to turn Wicken Fen into an immense laboratory for experimental ecology on a large scale.

Already reports of progress have begun to come from this laboratory in Godwin's studies of the level of the ground water surface.⁴ These records show the effect of rainfall, the seasonal drift and the rhythmical daily fluctuation for the years 1928-1930. A series of automatic water level recorders are described and their records are given. In addition, by the use of insert phytometers, transpiration is shown to be considerable and to be responsible for a fall in the fen water level during the day. Close to the drainage channels the level recovers at night but away from them the level remains permanently lowered, recovering only with rainfall.

The whole series of articles may be regarded as guide books along the way of ecological progress that may serve to stimulate similar experimental work in other lands.

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³ Godwin, H. The "sedge" and "litter" of Wicken Fen. *Jour. Ecol.*, 17: 148-160. 1929.

⁴ Godwin, H. Studies in the ecology of Wicken Fen. I. The ground water level of the fen. *Jour. Ecol.*, 19: 449-473. Figs. 1-20. 1931.

THE PLANT COMMUNITIES OF THE EARTH¹

For more than a half century Switzerland has had a notable group of scientists interested in the problems of plant life. Its most noted leader, Schröter, may be regarded as the founder of the Swiss school of geobotany which under his inspiring leadership has come to occupy a foremost place in Europe. There are no more distinguished geobotanists in the world than the group that honor Schröter as their teacher. Chief among them stands Rübel, a worthy successor of a great teacher, and the founder of the "Geobotanische Forschungsinstitute Rübel in Zürich."

Rübel's contributions to geobotany are so well known that a book from his pen attracts the attention of ecologists the world over. This volume itself seems to meet their expectations and must be regarded as a most important contribution to ecological science. While the author's most notable researches have been centered in the mountains of his native land he has travelled extensively and is able to write with the accuracy that comes from personal contact with the material described. The ecologists of America will recall his visits to the United States on the occasion of the International Phytogeographic Excursion of 1913 and of the Congress of Plant Sciences in 1926.

Rübel has also had the cooperation of Brockmann-Jerosch, a distinguished member of the Zürich school of geobotany, who has prepared a map of the climatic formation classes of the world reproduced and printed in ten colors. This map and Rübel's system of classification of plant communities attract attention at the first cursory glance through the volume.

The classification is a modification of that announced by Brockmann-Jerosch and Rübel in 1912² and is based on the physiognomy of the vegetation. It divides the plant communities of the world into three great types of vegetation: *Lignosa* or woody vegetation, *Herbosa* or herbaceous vegetation and *Deserta* or regions with little or no vegetation. These types are in turn separated into twenty-seven classes of formations.

The classes of the *Lignosa* are grouped in pairs, depending upon the height of the vegetation, and designated as forests or *silvae* and scrub or *fruticeta*. Thus the *Pluvilignosa* comprise *Pluviisilvae* or rain forests and *Pluviifruticeta* or such low rain tropic vegetation as mangrove swamps, dwarf palm (*Nipa*) and bamboo communities.

The next type, under laurel vegetation or *Laurilignosa*, includes *Laurisilvae* or forests where the dominant trees are dicotyledons with glossy evergreen leaves and protected buds and conifers of the more mesophytic types. These forests include the temperate rain forests of Chili and New Zealand, the laurel forests of Macronesia and the mesophytic conifer forests of the

¹ Rübel, Edward. *Pflanzengesellschaften der Erde*, pp. viii + 464, 242 figs., colored map. 1930. *Hans Huber, Berne & Berlin.*

² Brockmann-Jerosch, H. und E. Rübel. *Die Einteilung der Pflanzengesellschaften nach ökologisch-physiognomischen Gesichtspunkten*. *Leipzig*, pp. 72, 1912.

Pacific coast of North America which are characterized by *Sequoia sempervirens*, *Tsuga*, *Pseudotsuga*, *Abies*, *Thuja* and *Arbutus menziesii*. These forests pass into woody communities of lower stature, *Laurifruticeta*, which include laurel scrub of the Balkan Peninsula, the Rhododendron bush of the Caucasus and the Himalaya and the *Arbutus unedo* areas of the oceanic sections of the Mediterranean region.

In continental semi-tropical regions the *Laurilignosa* gives way to the *Durilignosa*, or broad sclerophyll vegetation. The *Durisilvae* or broad sclerophyll forest includes the *Quercus ilex* and *Q. suber* woods of the Mediterranean, the *Quercus-Arbutus* forests of the Pacific coast of the United States and certain *Encalyptus* forests of South Australia. Likewise the *Durifruticeta* embrace the sclerophyllous scrub of those regions designated locally as macchia, garigue, chaparral, phrygana, or fynbosch, and also some of the *Encalyptus-Acacia* scrub of Australia. The *Durifruticeta* is therefore a class that includes widely separated areas of great floristic diversity. It also shows a gradual transition to the next type of *Ericilignosa*.

In contrast with the preceding, the *Ericilignosa* presents great floristic uniformity, being sharply limited to Ericaceous heaths and appearing only in vegetation of lower growth included in the *Ericifruticeta*. These include arctic and alpine heaths, Mediterranean and South African scrub and areas of similar physiognomy in South America and Australia.

The *Aestilignosa* is the tropophytic woodland of the temperate regions of the world. It includes the well known deciduous forest or *Aestilsilvae* of the northern hemisphere and the deciduous bush communities of *Aestifruticeta* typically represented by hazel, birch and willow scrub.

Contrasted with the *Aestilignosa* which is in foliage during the summer is the *Hiemilignosa* where the trees shed their leaves during the hot dry summer. Here is to be placed the *Hiemisilvae* or monsoon forests most closely related to the tropical rain forest but with fewer epiphytes and lianas and a dominance of deciduous trees. In the *Hiemifruticeta* may be placed certain types of tropical scrub with a mixture of deciduous shrubs.

Last among the *Lignosa* types come the *Aciculignosa*, narrow sclerophyll or coniferous vegetation. The *Aciculisilvae* include the great conifer forests of the northern hemisphere with the exception of those already noted under the *Laurisilvae*. In addition to these climatic forests of the cooler regions there are others controlled by edaphic factors in various warmer climates such as the *Pinus palustris* forests and the *Taxodium distichum* swamps of the southern United States, and the *Pinus pinea* woods of the Mediterranean. The *Aciculifruticeta* includes the dwarfed pine and spruce of alpine regions and the *Juniperus* scrub of warmer and drier regions.

Herbosa are communities of grasses and herbaceous plants and are subdivided into two sub-types, *Terriherbosa* and *Aquiherbosa*, communities of dry land and those of swamps and ponds. Each sub-type includes three classes of formations.

The *Terriherbosa* includes *Duriherbosa*, *Sempervirentiherbosa* and *Altherbosa*. In the first of these the grasses and herbs have well developed mechanical tissues which give erectness to the plants that usually die down to the soil surface, during the winter. They are chiefly the grasslands of continental climates and include such formations as the tall, mixed and short grass prairies of North America and the corresponding communities of Eurasia. Some of the savannas of Africa are also included. The second of these classes, the *Sempervirentiherbosa*, in contrast, are dominated by plants that are mostly evergreen and that depend upon the turgor of their cells rather than upon mechanical tissues to maintain them in upright position. They are found in oceanic climates in temperate and cool regions and include certain grasslands in western Europe, in mountain regions and in tundra areas. The *Altherbosa* or tall herb communities often occur where forests have been destroyed, and in montane and subalpine localities where such plants as *Epilobium angustifolium*, *Heracleum lanatum* and *Mertensia ciliata* abound.

The *Aquiherbosa* include the *Emersiherbosa* which comprise the communities of fens (*Flachmoor*) sedge swamps, reed swamps (*Phragmitalia*), and salt marshes; the *Submersiherbosa* or submerged aquatic communities of both fresh and salt water; and the *Sphagniherbosa* (*Hochmoor*) or communities characterized by the presence and abundance of *Sphagnum* spp., by acid substrata and the formation of peat. All three classes are subject to much sub-division and these sub-divisions are discussed in detail.

Deserta comprise practically all open communities and are thus made to embrace many areas very different from those commonly regarded as desert, such as steppes, tundra, dunes and fell field. The *Siccideserta* are made to include all dry areas with open vegetation which may be conveniently divided into steppes where more than half the surface of the soil is covered by vegetation and deserts (in the usual sense) where less than half the surface is covered by vegetation. The steppes of North America are made to include communities of sage brush, shad scale, etc.

Frigorideserta, or cold deserts, include the open communities of cold arctic and alpine regions. They resemble deserts in physiognomy but include a much smaller proportion of annual plants. Mat plants, cushion plants and creeping plants abound here.

Litorideserta are deserts of the sea shore and include open stands of halophytes, while *Mobilideserta* include a variety of communities that remain open on account of the instability of the substratum. Here belong some of the associations of sand dunes, gravel slides, and alluvial fans. *Rupideserta*, including the communities of fell fields and rock crevices, and *Saxideserta* complete the list of classes of open communities. The last class includes the communities of lichens, mosses and algae on the surface of rocks and on the bark of trees.

This accounts for twenty-five of the twenty-seven classes of formations. The remaining classes are the *Phytoplankton* and *Phytoedaphon*, the micro-

scopic flora of the water and of the soil respectively. It will be seen that this classification stresses the close relationship of climate and vegetation, placing particular emphasis not only on the relationship of the habitat to the poles and the equator, but also to the distance of the habitat from large bodies of water giving oceanic, intermediate and continental types of climate.

Without attempting to criticise the classification as a whole, it may be asserted that it will certainly be fertile in stimulating suggestions. The subdivisions included in the various classes may be found subject to revision, for example, the position of the sage brush (*Artemisia tridentata*) community in the *Siccideserta* may be questioned since this scrub so often develops as a closed community. It may also be doubted whether the conifer forest of the Pacific coast of North America should be placed in the *Laurisilvae* rather than in the *Aciculisilvae*.

Under this classification with its many sub-divisions the plant communities of the world are exemplified and described in more or less detail. The alpine communities naturally receive special attention and their descriptions are more detailed. Photographs are used freely in illustrating the descriptions, many being from the camera of the author and his associates.

The vegetation map is probably the best available and serves excellently to give an idea of the original plant covering of the globe.

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KILIMANDJARO: ITS LAND AND ITS PEOPLE¹

An attractively presented account of a trip to the top of Kilimandjaro with extended notes on the plants, people, agriculture, general biology, physiography, and geology. Special attention is given to the Wadjagga and Masai, two strikingly different races, and to a general discussion of the belts of vegetation found on and about this great mountain.

Many of the major plant communities of Africa are found there. Good non-technical descriptions are given of the dum palm steppes, the river forests, the orchard steppes, the succulent steppes, and the Acacia steppes. Probably the most interesting are the descriptions and excellent photographs of vegetation at and above the timber line—the unique *S.necio*, *Lobelia*, *Erica*, and *Protea* growth, a veritable botanical fairyland. The author discusses at some length the plantations of banana, sisal, and coffee and such interesting plants as the baobab and *Sansiviera*, etc. A fund of information is given relative to the composition of many communities and also a short discussion of the plant geography. A special chapter is devoted to the animal life of the Masai steppe and to the termites.

The book is exceptionally readable, and adds material in both text and

¹ Geilinger, Walter. *Der Kilimandjaro: Sein Land und Seine Menschen.* 182 Textseiten mit 156 Abbildungen und vier Tafeln nach Autochromaufnahmen. Verlag Hans Huber, Bern-Berlin, 1931.

excellent photographs to the earlier and more classic works of Volkens and Myer.

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SEEDING AND PLANTING IN THE PRACTICE OF FORESTRY¹

Fifteen years have elapsed since the appearance of the first edition of "Seeding and Planting."² During these years "Seeding and Planting" has been the standard American work on the subject and has admirably fulfilled the purpose for which it was written. Within the past decade or so, however, there has developed in the United States and abroad, a really voluminous new literature on the subject. Most of the new information is contained in bulletins and in various reports and technical periodicals and frequently is not available to all, due to inaccessibility of the original publications or to the barrier set up by various foreign languages. The revised and enlarged edition of the older work is a response to the real need for bringing up to date present knowledge of seeding and planting in forestry. Both authors are widely known for their work in the field of plant science and each has made solid contributions to the literature of seeding and planting. It is indeed fortunate that the authorship of the second edition was in such competent hands. All responsibility for changes and additions in the new edition is assumed by the junior author.

The introduction deals clearly and briefly with the economic basis—the necessity—of seeding and planting. The rest of the book is divided into two parts, *the silvical and silvicultural basis* (chapters 2 to 5) and *the formation of forests by seeding and planting* (chapters 6 to 18). In chapter 2 is discussed the object of silviculture and the standard reproduction methods. This chapter, with the preceding, serve as an excellent basis for a review by students who earlier in their training may have studied the reproduction methods, or silvicultural systems as they are sometimes called. And such a review is really essential before beginning the study of seeding and planting. It is gratifying to note that at the very outset the authors stress the importance and practicability of natural reproduction. The popular conception of forestry within the United States unfortunately centers largely in artificial reproduction as a means of regenerating forest stands.

In chapters 3 and 4 choice of species in artificial regeneration and principles governing spacing are considered. A word of warning is issued against

¹ Toumey, James W. and Clarence F. Korstian. Seeding and planting in the practice of forestry, a manual for the guidance of forestry students, foresters, nurserymen, forest owners, and farmers. Second edition revised and enlarged, pp. xviii+507, text figures 162. John Wiley & Sons. 1931. Price \$5.00.

² Toumey, James W. Seeding and planting, a manual for the guidance of forestry students, foresters, nurserymen, forest owners, and farmers. First edition, pp. xxxvi+455, text figures 140. John Wiley & Sons. 1916.

the use of unproved exotics. In the past foresters have sometimes been indiscreet in their use of exotic trees for forest planting and outstanding failures have resulted. It is a question as to what justification we have for attempting to introduce exotics into American forests which are composed of so great a variety of excellent timber trees. Borthwick³ suggests that if an exotic tree fulfills any of the following conditions it may be worthy of cultivation.

1. If it is a species at present unrepresented, and is capable of producing timber of utility, or if it possesses advantages in rate of growth or is less exacting as regards soil and climate.
2. If it yields useful timber and is more resistant to indigenous enemies, e.g., fungi, insects, and animals, than those at present under cultivation.
3. If it possesses better quality as a shelter and nurse tree than those at present grown, i.e., if it offers silvicultural advantages to other species by association with them.

The principles which govern the composition of stands are enumerated in chapter 5. The relative merits of stands of pure and mixed composition are considered at length. It is true that successful establishment of mixed artificial stands calls for the highest type of silvicultural skill and this fact may account for the scarcity of such stands in America at present. Properly formed mixed stands, since they more closely resemble natural conditions and occupy the site more fully, have certain marked advantages over pure stands.

In chapter 6 (beginning part 2) the authors critically set forth the advantages and disadvantages of both natural and artificial regeneration. Costs, length of time required for establishment, and quality of resultant stands are all considered. Throughout the book, and in this chapter particularly, the authors stress the necessity of common sense and broad judgment in choosing and applying the methods described. Nursery and other silvicultural practice is essentially a local problem and usually must be worked out locally. Guiding principles may be laid down but the details of application must be decided upon by each practitioner after careful study of his own conditions.

Some foresters are of the opinion that in the United States we are now on the eve of a widespread planting program. Certainly federal, state, and private agencies are all directing more and more attention to regenerating lands now wholly idle or supporting very inferior growth. In recognition of this fairly well defined trend a chapter dealing with planting surveys and plans has been added in the edition under review. In the chapter which follows, collection, extraction, and storage of forest tree seed are considered. Recent years have seen marked advances in the methods of seed extraction and storage. Hand labor has been greatly reduced in the larger seed extractories with the introduction of various mechanical devices. The result

³ Borthwick, A. W. Tree frontiers. *Scottish For. Journal*, 41: 39-43. 1927.

is cheaper seed and probably, too, seed of generally higher quality. Several types of extractories are explained and easily understood plans for their construction presented. Seed quality and testing are discussed in chapter 9. The subject of seed quality, as related to its origin, has attracted widespread attention in recent years. It seems evident that in the long run the best source of seed for any given locality is the indigenous species of that locality. One may suggest that due to long association with the environment, the indigenous species of each locality have established a rather close adjustment to the complex of conditions which we call the habitat, and that this same close adjustment is commonly lacking in individuals introduced from other, particularly unlike, environments. In practice it will frequently be inconvenient or impossible to secure local seed. In these cases the seed should come from a locality in which the normal summer temperature closely corresponds with that of the locality where planting is to occur. In Sweden it is indicated that this difference in normal summer temperature should not exceed 0.5° C. (0.9° F.).

The protection of sites upon which artificial regeneration is being attempted is dealt with in chapter 10. Protection usually relates to such injurious agencies as fire, rodents, grazing and browsing animals, insects and fungi. The following chapter covers the preliminary treatment of seeding and planting sites. Many of the failures of artificial regeneration are directly traceable to lack of attention in this matter. Regeneration frequently has been attempted on unprepared sites where the soil or vegetational conditions were such as to practically condemn success at the outset. One may cite sand dune areas as an example of sites which usually require preliminary treatment before successful regeneration can be accomplished. The stabilization and reforestation of dunes in various parts of the world furnish many interesting examples of land reclamation on a large scale. Dwyer⁴ cites some extremely instructive cases of dune fixing and reforestation in South Africa. His paper, although not mentioned in the book under review, merits the attention of all interested in the reclamation of drift sands. In discussing accumulations of organic material in forest soils (p. 223) the authors use the terms *peat*, *dry mold*, and *raw humus* without clearly defining them. It is hoped that the recent appearance of Romell and Heiberg's⁵ work will tend to result in much clearer understanding and definition of the various humus layers in forests. In the past many terms have been loosely used.

In chapter 12 is discussed direct seeding as related to artificial establishment of forest stands. In the preface to the revised edition, prepared by the junior author, it is stated that in recent years nursery grown planting stock

⁴ Dwyer, E. B. Notes on reclamation of drift sands. *So. African Jour. of Sci.*, 25: 168-180. 1928.

⁵ Romell, L. G. and S. O. Heiberg. Types of humus layer in the forests of northeastern United States. *ECOLOGY*, 12: 567-608. 1931.

has largely replaced direct seeding in artificial regeneration within the United States, but that the chapter on direct seeding was retained in the new edition . . . "for completeness and for possible application on such of the more favorable sites in the United States as may need restocking artificially and on which direct seeding has been shown to result in a lower final unit cost per acre of successful regeneration." Now no one can deny that past results with direct seeding in the United States have, on the whole, been far less satisfactory than the results obtained through planting nursery grown stock. The reviewer, however, is not entirely ready to accept past results with direct seeding as proof that it may not serve as a very useful method of obtaining regeneration on certain forest lands. Many of the past tests were poorly considered and in the judgment of the reviewer, although possibly casting doubt on the general utility of direct seeding in American forestry, prove little more than that direct seeding requires considerable silvicultural skill and good judgment for successful application,—probably more than planting. The reviewer would like to see direct seeding given fairer and more careful tests than it has generally received in the United States. It is noticeable that in the references appended to the chapter on direct seeding in the new edition there is just one new reference, and that to work published in 1917. The recent work of Taylor,⁶ Robertson,⁷ Hedemann-Gade,⁸ Baldwin,⁹ and Schenstrom,¹⁰ to cite a few, has apparently been overlooked. Taylor indicates that in some cases planting costs nearly three times as much as direct seeding in Great Britain and remarks, "This difference in cost is striking, and the perseverance in the attempt to perfect a technique for direct seeding of conifers in Great Britain would, therefore, seem well worth while." Robertson in discussing direct seeding in New Brunswick, Canada states, "It would seem, therefore, that direct seeding can be done for less than half the cost of planting and the results would indicate that the method, far from being a failure, has a place to fill, and in its place can economically replace planting." Hedemann-Gade estimates that in Sweden, which is one of the present day leaders in European forestry, between two-fifths and one-half of the annual expenditure for forest cultivation is devoted to direct seeding.

Chapter 13 is concerned with the selection and development of the forest nursery site. The one following deals with preparation of nursery seed beds and seedling culture. Both of these chapters are authoritative and in addition to containing the best American and European information, reflect the

⁶ Taylor, W. L. Direct sowing of conifer seed. *Empire For. Jour.*, 4: 106-110. 1925.

⁷ Robertson, W. M. Analysis of direct seeding methods. *Jour. of For.*, 24: 260-264. 1926.

⁸ Hedemann-Gade, E. Undersökningar angående lämpligaste tiden för sådd av barrträdsfrö. (English summary.) *Svenska Skogsvidrsföreningens Tidskrift*, 25: 5-50. 1927.

⁹ Baldwin, H. I. Can direct seeding succeed in New England? *New Hampshire Forests*, 6(2): 13-15. 1929.

¹⁰ Schenstrom, S. R. A study of reforestation by seeding. *Forestry Chronicle*, 6: 173-182. 1930.

wide forest nursery experience of the authors themselves. In recent years there have been many interesting applications of mechanical appliances in nursery practice. Hand labor has been practically dispensed with in certain operations. Transplanting and distribution of nursery stock is the subject of chapter 15 and is followed by a discussion of nursery diseases and injuries. The treatment of pathological and entomological nursery troubles will be of interest and assistance to all engaged in nursery work. The last two chapters take up forest planting material, seasons of planting and spacing (chapter 17) and planting methods and technique (chapter 18).

The chief value of the book is probably as a text in courses dealing with seeding and planting in forestry. The student will find the information under each subject carefully classified; the use of bold face type for sub-heads and the practice of italicizing important statements are further devices which make the book especially usable as a text. Figures are liberally supplied (162 in all) and, with very few exceptions, are of distinct value in engaging the interest of the reader and in clarifying the text. Useful tables containing a wealth of information are found throughout the book. At the end of each chapter there is appended a list of the more important references to the subject. These lists will be welcomed by workers who have occasion to use the book as a reference, and by the occasional ambitious student who wishes to refer to the original literature. Although the lists are certainly ample for student use the investigator who is using the book for reference may occasionally regret that they are not longer.

"Seeding and planting in the practice of forestry" is exactly what it purports to be, "A manual for the guidance of forestry students, foresters, nurserymen, forest owners, and farmers." The book promises to exert as much, or greater, influence upon the development of seeding and planting practice within the United States during the next fifteen years as its predecessor has during the past fifteen.

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INSECTS AND CLIMATE¹

In 1907 Bachmetjew² wrote a monumental work upon the effects of environmental factors upon insects, in which he summarized the literature upon the subject. Since that time no one has attempted to cover that ground until Uvarov wrote the paper which is the subject of the present review. The task was one of great magnitude. Uvarov read and abstracted about 1300 books and papers, and after rejecting some of them, summarized about 1150. He has produced out of chaos a degree of order so great that his paper may be regarded as a textbook on the subject.

¹ Uvarov, B. P. Insects and climate. *Trans. Ent. Soc. London*, 79(1): 1-247, illus. 1931.

² Bachmetjew, P. Experimentelle entomologische Studien, Bd. 2, *Sophia*, 1907.

The paper is divided into two sections. In the first part the various factors are considered largely from a physiological and laboratory standpoint, and the many hypotheses that have been put forth to explain their effects are examined critically. Heat, Humidity, Other Factors, and Combinations of Several Factors form his main headings. Quite naturally over two-thirds of the section is devoted to heat, as this is the factor with which most work has been done. He presents and examines the several expressions for the relation of temperature to rate of development, from the old "thermal constant" to the newest catenary curves of Janisch, and concludes that the case is not yet proven for any particular curve. He stresses the lack of knowledge regarding the body temperatures of poikilothermal animals, and shows that this must be considered in any discussion of heat utilization. Measurements of external temperatures are at best crude approximations to the body temperature of the animal. This is all perfectly true from the standpoint of the physiologist, but from that of the ecologist it seems to me that external temperatures are what will have to be used in practical work.

At various places throughout the paper he has placed little paragraphs of introduction or summary that are very keen comments upon the points in question, and worthy of further elaboration. For example, under the heading "Combinations of Several Factors" (p. 80) he says:

"An insect living under natural conditions is never exposed to one isolated climatic factor, but to the continually changing combinations of several. While in the study of the responses of an insect to environment it is necessary first to apply the analytical method, and to investigate the influence of each factor separately, it would be wrong to assume that the response of an insect to the combined action of several factors will represent merely a sum of the responses to each of the factors involved. Indeed, we must first satisfy ourselves whether this is true, or not, by studying experimentally all the more usual combinations of factors."

"Unfortunately, as will be seen from the following pages, very little work has been done in this direction."

The second part of the paper considers weather, climate and insects. In this part the data are largely taken from field studies, and the results are discussed from a field standpoint. His main headings are Relation of Weather to the Activities of Insects, Daily and Annual Cycles, Climate and Distribution, Effect of Climate on Abundance, and Climate and Weather in Economic Entomology. There are so many interesting topics discussed in this section that it is only possible to select a few for mention here.

In the part on annual cycles there is a very interesting discussion of dormancy and diapauses, in which a few rather puzzling specific instances are noted. On page 106 the case of *Operophtera brumata* Linn. is mentioned. The adults fly in the fall, and fly much earlier in more northern and cooler areas than they do in more southern and warmer areas. Uvarov offers no explanation of this variation, and has apparently missed a paper by Crumb

(1926, Proc. Ent. Soc. Washington, 28 (9): 201-207) on *Nephelodes emmodonia* Cram. This species shows a similar relation to temperature, which Crumb shows to be explained by a prepupal dormant period in which the normal temperature relation is reversed, as the prepupal period is longer at higher temperatures, and thus retards emergence.

In his discussion of climate and distribution, Uvarov stresses the necessity for further study of ecoclimates and microclimates. With this idea the present writer is in hearty agreement. It is only by the careful study of environmental conditions at the exact spot where the animal lives that further progress will be made in the untangling of interrelations in ecological communities. However, in broader studies, where entire communities are the units of study, the microclimate may be regarded as indicated by the presence of a particular community, and the general climate under which that community flourishes becomes of greater importance. At times when general conditions are unfavorable, species and communities maintain their existence in isolated "ecological islands," where local conditions of soil or exposure remain more favorable, and at times of outbreaks the climate of these islands becomes the general climate of the region. Many workers, seeking for the climatic causes of outbreaks, have made such detailed studies of microclimates and specific conditions that they have lost sight of this fact.

Uvarov, in discussing the course of outbreaks, has crystallized the nomenclature for the various phases. Following several German workers, he recognizes a "preparatory" year or period, when the insect is localized and quiescent, a "prodromal" period, when the insect is rapidly increasing, and a period of "eruption" or "outbreak." The outbreak is followed by a period of decreasing population, and the present writer suggests the term "recessive" for this period.

On pages 160-162 he has a very interesting discussion of balance in nature. He makes several direct hits at the current notion that living organisms are in stable equilibrium. The usual course of events is a continuing series of fluctuations, never even hesitating at a theoretical "normal" population, which is a fiction. The analogy to a pendulum must be corrected in two ways. First, the fluctuations are irregular, both in velocity and magnitude, and, second, the point of suspension also fluctuates irregularly. The "balance" as depending upon food and enemies, must be changed to one dependent chiefly on climatic factors, with food and enemies furnishing minor fluctuations.

On pages 170 et seq. Uvarov discusses various diagrams used for analyzing meteorological data. The most useful of these is undoubtedly the climograph of Ball, and its variant, the hythergraph of Taylor. Uvarov terms the former a "climatograph," which is rather unfortunate, as Munns (1922, U. S. Mon. Weather Rev., 50: 477-481) uses the same term to describe a somewhat similar chart plotted on polar coordinates. This graph has been used very little in bioclimatic work, but properly deserves the name climatograph.

Personally I can see very little value in drawing a distinction between "climograph" and "hythergraph." Both refer to the plotting of heat against moisture, connecting the points for a time cycle of some sort, and, since climograph is the older term, it might be used for all such diagrams.

On page 174 is an interesting discussion of the blind use of statistical methods in weather analyses. He makes the very pertinent statement that mathematical methods have their limitations, and may even become misleading, unless used intelligently. His point is well taken. When I was "young and foolish" I had a more or less blind faith in statistics, which an acquaintance with a wide variety of problems has somewhat shaken. An advanced statistical analysis has its place in the preliminary analysis of a very complex problem, but the findings of such an analysis must be supported by much independent evidence, and especially by common sense, before they can be completely accepted. At present, I believe that the most useful function of statistical analysis is to furnish numerical values for trends and factors whose existence is amply demonstrated in other ways.

The section on forecasting of distribution and abundance is very interesting, and indicates what the future may hold in this direction.

Considering the paper as a whole, it is evident that Uvarov has very ably collected and edited the literature upon a very complex branch of ecology, and has produced a work of immense value to all workers concerned with bioclimatics. His summaries and comments are especially valuable, and it is regrettable that the nature of the paper did not allow him to express his own opinions more fully.

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NOTES AND COMMENT

A RECORDING ATMOMETER

The use of the atmometer for ecological studies has become quite general and its value is well recognized. It has, however, certain disadvantages, one of which is the expense of daily attention where such records are kept and the instruments are distributed at widely separated field stations.

To overcome this difficulty a device has been developed that records the evaporation over the period of a week. The instrument as shown in the accompanying illustration consists of a cylinder containing water on the surface of which floats a flat, cylindrical, hollow metal float. To the top of this float is firmly soldered a square metal rod that passes upward loosely through a square guide opening. On the upper end of the rod is fastened a weak spring carrying a pen. The spring can be bent so as to touch lightly the surface of record sheet and the square shape of the rod and guide prevents turning as the float lowers.

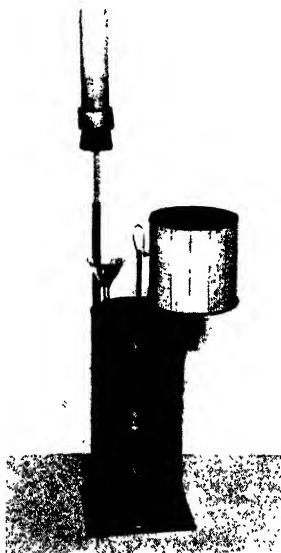


FIG. 1. Recording atmometer.

The record sheet is carried on a standard clock drum such as used in other recording instruments. It registers continuously in cubic centimeters of water lost. This drum is geared to a metal block fastened to the side of the water reservoir.

The atmometer cup is carried on a glass tube that fits tightly into a metal tube and extends to the bottom of the reservoir. The tank can be made of such size that it will hold enough water for seven or eight days during the driest period of the year.

To prevent injury to the clock and the record sheet by rain the entire instrument is placed in a galvanized can with a tight fitting conical top through which the atmometer cup projects. This top can be raised to change the record and refill the cylinder.

While the apparatus still has certain imperfections, it has been used successfully during the past season.

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AN INSTANCE OF THE IMPORTANCE OF H⁺-ION CONTROL IN
OSMO-REGULATION STUDIES

Experiments with common river-crabs of the genus *Paratelphusa* M. Edw., carried out at Bangkok, Siam, in 1930, demonstrated that these crabs are capable of living more than twenty-four hours after transfer from fresh water to artificial sea water. In other words, while normally living in a medium of extremely low osmotic pressure, they survived a transfer (without intermediate stages) to one of over twenty atmospheres osmotic pressure.

Several individuals collected and studied at Nan, in northern Siam, about a thousand feet above sea-level and more than three hundred miles from the Gulf of Siam, survived the same treatment as those studied in Bangkok.

The Bangkok specimens were subjected, subsequently, to a sucrose solution isotonic with the artificial sea water. In this medium, however, all individuals died within six to eight hours. It occurred to me that the difference in pH between the two media might be the explanation of the difference in results. Tests showed that the sucrose solution was quite acid (about pH 4), whereas the artificial sea water was of about pH 10. The sucrose solution was then adjusted to pH 10 by the addition of NaOH, and crabs placed in this medium. These survived twenty-four hours, as had those in the artificial sea water. In other words, their survival in a medium of higher osmotic pressure depended, at least partly, on the H⁺-ion concentration of the new medium.

There may be here a suggestion of an explanation for some peculiar results obtained by Adolph¹ while studying crustacea of the genus *Gammarus*. According to Adolph, a fresh-water species of *Gammarus* survived 100 per cent sea water for five hours, and a marine species of the same genus lived five hours in sea water diluted to 0.5 per cent with distilled water. On the other hand, the maximum concentration of sucrose in which the fresh-water species survived five hours was 0.30 molar, the osmotic pressure of this medium being little more than one-third that of sea water. The marine form survived five hours in a medium consisting of 15 per cent sea water and 85 per cent 0.88 molar sucrose—the maximum concentration of isotonic sucrose tolerated for the period of time selected. The fresh-water form, having survived 100 per cent sea water, should have survived 0.88 molar sucrose as easily as 0.30; whereas the marine species should have shown a survival concentration of not less than 100 per cent 0.88 molar, since that was isotonic with the sea water employed in the experiments. In both cases, it seems obvious that one is not dealing with a problem of osmo-regulation alone.

Two generalizations in the above-mentioned paper are, for *Gammarus* at least, based on studies with media in which the pH was not controlled, and in which it may have been very different from that of sea water. These conclusions were first, "that for freshwater organisms the osmotic pressure of the medium usually limits survival, while for marine organisms a great range of concentrations can be resisted"; and, second, that "we can . . . probably regard the maximum survival concentration for freshwater animals as a measure of the osmotic pressure of their body fluids." In applying the second generalization to *Gammarus* we are left with the dilemma of choosing between the osmotic pressure of sea water and that of 0.30 molar sucrose as the measure of the osmotic pressure of the body fluids. The first generalization, it seems to the writer, is also unjustified. Certainly exceptions

¹ Adolph, Edw. F. 1925. Some physiological distinctions between freshwater and marine organisms. *Biol. Bull.*, 48: 327-335.

exist. Pearse² studied the survival of various marine invertebrates in dilute sea water, and found marked differences between related forms. Lobsters are commonly killed by collectors, quickly and easily by immersion in fresh water. And yet the fresh-water crabs which I studied survive for twenty-four hours in sea water. It is therefore not true in general that the marine forms resist a great range of concentration while the fresh-water forms are limited in this respect. Conclusions regarding osmo-regulation can not be based on experiments with solutions in which the osmotic pressure alone is considered.

In passing, I should state that the canal water at Bangkok, in which the crabs lived, was probably never so basic as the pH 10 of the experiments cited. The results of several tests indicate that the pH of the canal water varied from about 7.5 to over 8.5, this variation apparently correlated with the photosynthetic activity of the aquatic plants. The water in these canals became slightly brackish during the dry season, but the water at Nan was always distinctly fresh.

Further analysis of this interesting problem was not carried out, these observations being submitted for their value in indicating how necessary it is to control the reaction of the medium in experiments on osmo-regulation.

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AN UNUSUAL LIVING INCLUSION IN THE SHELL OF A CLAM

In the early summer of 1929, a dealer in clams in Cambridge gave the writer the left valve of a *Mya arenaria* Linn. that had come into his hands as part of a living clam from Ipswich, Massachusetts. It was remarkable in that from end to end it was run through by a rhizome, also living at the time, of the common cord-grass, *Spartina alterniflora*, Loisel. The inner and outer views of this unusual specimen are given in the photographs reproduced in Figs. 1 and 2.

In Fig. 1, it can be seen that the rhizome enters the substance of the valve at the posterior end of that structure in a region where the lines of growth are somewhat broken and emerges from the valve between the corresponding lines at its anterior end. From the region of entrance to that of exit, the outer surface of the valve shows no evidence of the rhizome. In Fig. 2, the interior of the valve is seen marked by a low, broad ridge running from anterior to posterior and indicating the part of the valve occupied by the rhizome. The layer of nacre that forms the ridge was accidentally broken through near its anterior end, and shows the substance of the grass plant that fills the canal under the ridge. As can be seen in the photograph, the nacre is relatively thick. It represents the most recent deposit of this material by the clam which thus attempted to protect its own living substance from the invading grass stem.

The way in which this strange combination was produced may be outlined as follows. The clam at the time it was killed was probably a little over three years old. This age is inferred from the bands of winter growth, three of which appear on the outer surface of the valve (Fig. 1). The total length of the valve in its present condition is 75 mm. The clam was probably hatched in June 1926 and the growth lines of the following winter show that at that time the valve had a length of a little over 44 mm., which agrees well with the average size of the first-year valves of this species, as recorded by Mead.¹ The second set of winter growth-lines, those for 1927-1928, indicates a valve length of about 61 mm., and the third set, 1928-1929, a length of 69 mm. This last set is followed peripherally by a narrow band of rapid summer growth which reaches the present edge of the valve, a

² Pearse, A. S. 1928. On the ability of certain marine invertebrates to live in diluted sea water. *Biol. Bull.*, 54: 405-409.

¹ Mead, A. D. 1900. Observations on the soft-shell clam. *Ann. Rep. Comm. Inland Fisheries, Rhode Island*, 13, 1-25.

growth that terminated with the death of the clam at the hands of the dealer in the early summer of 1929. As already stated, the final length of the valve is 75 mm.

When the regions of entrance and of exit of the grass stem into the valve are noted in relation to the lines of growth, it is seen that the stem must have entered the valve directly after its last winter growth in 1929. In the late winter or early spring of that year, the growing grass stem must have thrust its head in between the mantle and the shell at the posterior edge of the valve. This entrance may have been facilitated by an injury which the posterior

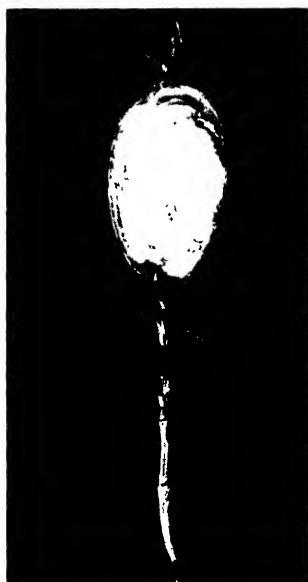


FIG. 1. External view of the left valve of *Mya arenaria*, showing the rhizome of cord-grass, *Spartina alterniflora*, passing into and out of the valve. Antero-posterior length of the valve, 75 mm.



FIG. 2. Internal view of the left valve of *Mya arenaria*, showing the ridge and, where it is broken into, the canal through which the rhizome of the cord-grass passes.

edge of the valve apparently suffered at that time. After this entrance, the stem must have grown anteriorly over the space between the mantle and the shell till it met the anterior edge of attachment between mantle and valve, through which it forced its way to the exterior. Beyond this point, judging from the condition of the specimen, the grass grew very little. Meanwhile, the mantle had covered the whole interior of the valve with a considerable layer of nacre as a protection, thus forming the canal through which the rhizome passed. This whole reconstruction must have taken place between the late winter and early summer of 1929 and shows how vigorous and active such processes are.

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BASIC PRINCIPLES OF THE CLASSIFICATION OF COMMUNITIES AND HABITATS AND THE USE OF TERMS¹

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INTRODUCTION

In any attempt to clarify the use of terms in modern ecology, foremost attention must be given to the youth of the subject. Modern ecology is essentially only forty years old. Most of the men who have contributed to the field are still living. When they first began to use terms, the number of aggregations of animals and plants which they had seen and studied was obviously much less than they had observed twenty or more years later. If the investigators are progressive men, their use of terms may of necessity be modified with more knowledge and experience. In some cases they will have the results of further studies nearly ready for publication at the very moment a colleague's paper appears citing them as authority for nomenclature, the abandonment of which they are about to announce. So long as this condition exists, it would seem wise to consult the men working in the field whose nomenclature is to be discussed. Organizations such as the Ecological Society of America could greatly facilitate the development of rational nomenclature by keeping a list of members in the fields requiring its use and encouraging discussion among them.

Classification of communities² is dependent upon the development of clear concepts of these aggregations themselves. At this point the students of the past, who are the investigators of the present, were poorly prepared; they did not get good *scholastic* training in concepts of natural communities. They were trained in anatomy and a little physiology and dealt to a large degree with adaptations and life histories instead of *communities* and the major producents and consument *niches* within communities. Instead of choosing the dominant or *influent* or even the abundant organisms for his physiological

¹ Contribution from the Zoological Laboratories of the University of Illinois No. 420.

² A community includes all the plants and animals of an area.

and life history studies, the investigator of this school has sought those of peculiar interest, easy to obtain, or those which chance to be at hand.

Courses of instruction in ecology have been and are still too few and, still worse, too superficial. The body of material which might be brought into such courses was very small at the time of initial course making. It is still far from comprehensive. On the animal side, courses which deal with all the population of areas (representing communities) are rarely available and, where quasi-ecological work is given, comprehensive courses dealing with the community are usually not presented. Instead, there is a course on insects, one on the lower vertebrates, a course on birds and occasionally also one on mammals, usually largely taxonomy and simple natural history. These are a necessary part of the training of one going into ecological work, but should be preceded by a course which has taught the student how to evaluate these groups in actual communities. The usefulness of most of these courses for ecologists could be greatly increased by a broadening of view point in the direction of ecological values.

One of the outstanding difficulties in the development of ecology is the method of dealing with the results of scientific expeditions of which there have been a very large number. The expedition usually carries specialists only in certain groups of organisms, some groups being omitted entirely. Some expeditions specialize on birds, some on mammals, some on reptiles and amphibians, and some on insects. Such is the condition viewed from the animal side, and it is, doubtless, paralleled from the plant side, though possibly on a smaller scale. Where an expedition has been of a general character, as well as in the other cases enumerated, the specimens obtained have been sent to numerous specialists with a view to the development of taxonomic work, including the description of new species and listing of new localities of occurrence. This is an important and essential procedure, to which there can be no objection, but no one has been charged with giving the scientific public any knowledge of the aggregations of organisms which were found by the expedition, and the evidences of communities have largely been lost. This is in part a necessary result of the failure to do even quasi-quantitative work. Such quantitative observations as might have been made are commonly lost, and all associative occurrence of species obliterated.

The taxonomic method of listing organisms is hopeless from the standpoint of modern ecology. The writer is familiar with a Pacific coast town in which there are five hundred whites, twenty-five American Indians, three Mongolians, and one Ethiopian. Thus, the taxonomist lists the human population (Linné, 1788, pp. 21-23) of Known Port:

<i>Homo sapiens europaeus</i> Linn.	Known Port	British Columbia
<i>Homo sapiens americanus</i> Linn.	Known Port	British Columbia
<i>Homo sapiens asiaticus</i> Linn.	Known Port	British Columbia
<i>Homo sapiens afer</i> Linn.	Known Port	British Columbia

Such listing of varieties or species gives the reader no idea as to whether this is a white settlement, an Indian settlement, or a Negro settlement. Taxonomists frequently say that abundance is no part of their field and that they care nothing about it. Their object is to find and list all the kinds from each locality. Taxonomy properly used is the chief aid of ecological work, but at the same time, because of its improper methods, it is one of the chief stumbling blocks to first class ecological work.

PRINCIPLES OF CLASSIFICATION

Ecological classification consists in (1) *evaluating organisms within communities*, (2) *recognizing communities* on the basis of *important organisms*, and (3) *evaluating and arranging the smaller and larger communities* with reference to each other. The latter must be carried out with reference to the largest natural units (Biotic Formations).

1. *The Evaluation and Classification of Organisms within the Community*

The importance of the abundant or otherwise significant species, commonly referred to as dominants, influents, subinfluents, subdominants, etc., is great. The rarer species play no important rôle in biotic interaction; incidental and accidental species should be given little or no consideration. The underlying cause of the failure to evaluate community constituents is to be found in the fact that most workers are specialists in particular taxonomic groups and tend to emphasize either the large or the small organisms as the case may be. In the original communities on land, especially, various animal groups given in the order of their ecological importance are probably, first, mammals; second, birds; third, insects and other arthropods; and fourth, reptiles and amphibia. The significance of the different groups varies with the climate and other conditions. The evaluation of plants does not follow the taxonomic series as closely as that of animals, but is much more closely related to size and form.

Contrary to the frequent practice and common dictums, the investigator of a community must become a *specialist* on 150 to 200 species of plants and animals distributed in all the taxonomic groups represented, rather than a specialist upon some division of the plant or animal kingdom.

2. *Classification of Communities on the Basis of Important Organisms*

Classification of communities must go hand in hand with the evaluation of the organisms which constitute them. The limits of a community are determined by the *limits of the dominance and influence of its outstanding species*, not by the occurrence of rare, interesting, or even characteristic species. Characteristic species, however, are important indicators. The question of whether the habitat or the community shall be emphasized in classification demands first attention. A safe criterion here may be illustrated by another

example from human population. Let us imagine that in some city the colored district happens to be in the low ground next to a river. When we go to the next city, the negro district is in proximity to a railroad, so that the use of habitat here would hardly serve the purpose. Furthermore, everybody recognizes that the negro district is the section in which the population is *predominantly negro*. This holds good wherever aggregations of human population occur. One can conceive, however, of very thinly settled districts in which there are only occasional negroes and occasional whites so widely separated that a community can hardly be recognized, especially where the occurrence of the population is unstable.

As a general rule, where a definite assemblage of organisms can be used, the organisms rather than the habitat should be followed. This is well illustrated by an intertidal community commonly dominated by barnacles. One frequently sees articles in which these barnacle communities are treated as communities on rock, communities on wood or piling and occasionally on metal. In the localities in which the author has made intensive studies, there is essentially no difference as regards dominants between the communities on wood and the communities on rock or metal, provided the objects to which the organisms are attached have been in the water the same length of time, and the decay of the wood or disintegration of the rock has not caused the aggregation to loosen and fall off. Other examples chosen from the sea would serve to illustrate the fact that the more abundant animals often occur over various kinds of bottom ranging from rock to hard mud. The sessile animals are less abundant in mud, but occur on shells scattered above the mud.

In fresh water streams with shifting bottom, *communities* can hardly be said to occur. It is only in favorable places that stability lasts long enough to enable them to develop. The stream bottom is always kept in an early developmental state so far as communities are concerned. One may compare it to the condition of sand dunes on land, where the constant shifting of sand always leaves the initial successional stages of plant communities, while late successional stages ordinarily constitute a very small proportion of the dune area. Under the conditions common in streams and the early developmental stages of sand dunes and comparable situations, it may possibly be tenable to use the habitat instead of the community, because the use of the community under the existing state of knowledge may be fully as confusing as the use of habitat. In all late stages of community development, the organisms rather than the habitat should always be used. The tendency during development, however, is always toward uniformity, *i.e.*, of soil and bottom materials. It is best to classify the stages in accord with the ultimate condition of the community, because it is much more uniform over large areas than the substratum. Climax communities on land may be found commonly on all types of initial soil. This is the basis for the general principle that climaxes are climatic.

a. The Integrity of the Area

One of the first principles in classifying either communities or habitats is the integrity of the area. In all terrestrial communities the primary aggregations of life must be concerned with all the organisms of the earth's surface contained within an area. This is the first principle of ecological treatment of scientific data. The same is true of intertidal areas and of the bottoms of bodies of water or the organisms immediately above it, which may be taken to correspond to birds and mammals on land. It is only in comparatively deep water that truly pelagic communities must be recognized (Murray and Hjort, '12). It is probably only in the deep sea that primary communities and primary habitats may be recognized one above the other, due to great depth and the large vertical difference in physical factors and to a complete change in the important species of organisms. The recognition of primary divisions of communities or habitats on land and in shallow water on the basis of layers within the community is supported by little or no tenable evidence. The plants of the lower layers of a community can rarely grow without the protection of the taller plants. Many birds, mammals and insects are directly or indirectly very influent in *all* the layers of the average terrestrial community. Animals which feed upon the ground surface may be influent in their action on tree seeds and seedlings even though they never go into the forest crown. Most of the community constituents do not stay in one layer, but move up and down from layer to layer. This is what makes the layers secondary.

Making of primary divisions on the basis of layers or levels as, for example, the soil, the ground surface, the vegetation and the atmosphere about the vegetation, cuts across the bodies of the dominant plants. Animals commonly migrate from one of these divisions to the other and back again, every twenty-four hours in many cases, and sometimes much oftener (Pearse, '26, Chap. 7).

3. Classification and Evaluation of the Larger and Smaller Communities

Classification of communities has hitherto been undertaken from three viewpoints. The first of these is concerned largely with groups originating as the offspring of single parents, or other aggregations composed chiefly of one species. Investigators interested from this viewpoint have attempted to classify the aggregations as to their origin, the relations of the individuals, etc. Some of these aggregations, especially of the social insects, have commonly been called societies, though they are, strictly speaking, families, as Read ('20, p. 36) has pointed out. Some of these families are very complex. The permanently immature offspring do the work in taking care of the young (Allee, '30; Wheeler, '28).

Classifications from their point of view have rarely gotten beyond the family with its guests, pests and a few associates. Workers have occasionally

referred to the animals associated with these colonies, taken with the colonies themselves, as an "association," but there have been no attempts to synthesize these small groupings with the large natural units described below. It must be recognized also that the studies of specialists on particular taxonomic groups have frequently classified the unnatural aggregations, which they often mention, more nearly on this basis than on the second one.

The second viewpoint and method of procedure are altogether different. Very large areas covering millions of square miles are regarded as primary units and the aim is to evaluate all the large and small assemblages of individuals of which the primary assemblage is composed.

It is true that many workers from this viewpoint have studied only small subordinate communities and have not evaluated them in the large natural units to which they belong. This fault results chiefly from lack of comprehensive studies of the larger natural areas. These shortcomings have been further emphasized by limiting attention strictly to the small community considered. These two faults have resulted in a loose use of terms and at the same time in little need for some terms, *e.g.*, Faciation, Lociation (table I), which are quite important when the variations in the community are brought out through travel and study over wide areas.

Consideration must, however, be had for the size of a community. The use of the same term for rocks moistened by dripping water and for the whole abyssal bottom of the sea (Klugh, '23, pp. 371 and 373) is difficult of defense. The ocean floor, because of its great age, must be assumed to be a climax community, while the rocks moistened with dripping water are local and usually unstable. There are many difficulties in the use of area covered, before the nature and extent of the climaxes has been determined.

The fresh water hydrobiologists, especially the limnologists, have developed a third type of nomenclature based more upon the habitat than on the biotic communities. It is well demonstrated that nearly all small fresh water communities are undergoing or may at any time begin succession toward the climatic terrestrial climax of the area. This makes them a part of the natural system suggested in the first three columns of table I. However, there has been almost no attempt to build up a nomenclature having any relation to the large terrestrial climaxes.

The largest natural unit is the biome or biotic formation. These are roughly represented by the large areas of deciduous forest, grassland, tundra, etc., which characterize the North American continent. Table I shows illustrative magnitudes of grassland communities based largely upon plants.

Table I shows illustrative magnitudes for the grassland communities, as illustrated by Shantz (Shantz and Zon, '24) and Clements ('20), and for the marine communities of the North Atlantic as shown by Davis ('23) and Peterson and colleagues (Peterson, '14; Jensen, '19, p. 33).

TABLE I. *Community classification*

Climax communities	On land		Sea benthic	
	Magnitude of area covered	Condition	Magnitude of area covered	Condition
1. Biome or biotic formation	1,000,000 sq. mi.	Usually continuous	10,000 sq. mi.	Usually continuous
2. Association	100,000 sq. mi.	Usually broken by 7	5,000 sq. mi.	Continuous
3. Consociation	100 sq. mi.	Continuous	100 sq. mi.	Continuous or fragmented
4. Faciation	10,000 sq. mi.	Broken by 7 or 8	100 sq. mi.	Broken
5. Lociation	1 sq. mi.	Continuous	2 sq. yd.	Continuous
6. Clan	4 sq. yd.	Continuous	0.5 sq. yd.	Continuous
Developmental communities	Terrestrial xeric		Terrestrial hydric	
	Size	Condition	Size	Condition
7. Associes	10,000 sq. mi.	Continuous	100 sq. mi.	Fragmented
8. Consocies	100 sq. mi.	Continuous	Small	Fragmented
9. Facies	1,000 sq. mi.	Continuous	10 sq. mi.	Fragmented
10. Locies	1 sq. mi.	Continuous	1 sq. mi.	Fragmented

All the smaller communities mentioned in table I, both developmental and climax, lie within and constitute the biome or biotic formation, and many of the smaller communities lie within the larger ones. The purpose of the table is merely to give some idea of the size of the various units. Their significance cannot be elucidated here. In addition to size differences, there are differences in stability both secular and seasonal.

4. Classification as to Stability

a. Secular Stability

It is well established that communities develop on denuded areas. The final and most stable stage is the climax. Stability is an important consideration in the ranking of communities on land. The climax is more stable than the developmental stages. There are fewer seasonal species of animals and more that are classed as perennials, hence some consideration of stability enters into the division into *developmental* and *climax* communities. Climax communities are relatively stable, but still are microcosms and are undergoing change. Developmental communities change more or less rapidly, have a greater number of seasonal animals and are probably subject to greater fluc-

tuations in total of small non-dominant plants and animals. *Developing communities are subordinate to climax or relatively final communities.*

Succession and climax have to be taken into account in ecological classification, though, speaking in general terms, development has to be substituted for succession, for in occasional plant communities and in many marine aquatic communities a climax is reached through the addition of species without any being lost. However, the principle of development and climax constitutes the only basis in natural law and order for the recognition of major community areas. The facts in general are recognized by ecologists; for example, no plant ecologist doubts that deciduous forest comes in on good soils lying midway between the dry sand ridges and the swamps of the coniferous forest area of the coastal plain of southeastern United States. This is taken to indicate that after a very long period the deciduous forest would take possession of the entire southeastern coniferous forest area. A few plant ecologists maintain that this is a fact relatively insignificant as compared with the proper classification of the present condition of the area, as shown by its actual present soil and vegetation. The development of communities and the climax seem to exemplify the only natural law which may be followed in this case. Therefore, scientifically speaking, it should be followed, and this in no way hinders the treatment of the area as a coniferous forest on poor soil, which represents an initial or early stage of the development of a deciduous forest. Many of the difficulties and disagreements of plant ecologists could readily be smoothed out by consideration of the relations of animals in this connection. Animals of great importance in the deciduous forest, such as the Virginia deer, gray fox, opossum, wild turkey, and a great number of other important birds and mammals, belong primarily to the deciduous forest and range throughout not only the climax but also the subclimax coniferous areas much as if they were actually deciduous forest already. If natural laws and dynamic principles are not to be the basis of classification, we must fall back upon aims or subjective fancies, and arbitrary categories (Dahl, '33; Hancock, '11).

b. Seasonal Instability—Seasonal Communities

The second type of instability is concerned with seasonal additions to the perennial population present throughout the year. A part of these might be called seasonal boarders, especially the birds, while the seasonal plants and insects of land communities act as food for them. The seasonal changes in population may preferably be represented according to Blegvad's method as shown in fig. 1. This is redrawn and modified for the second year from Bird's ('30) Manitoba data. In this locality there are fewer seasonal groups, comparable to summer and later winter boarders, housed among the perennial population of a California coast resort town. Seasonal communities are subordinate to both climatic and developmental communities.

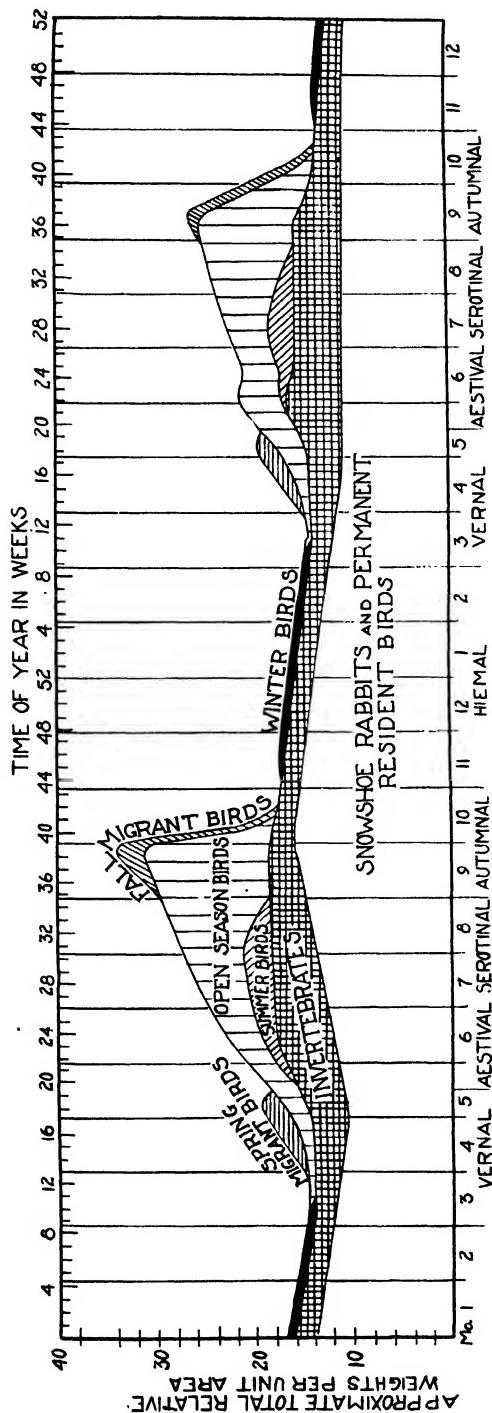


Fig. 1. The biological seasons and seasonal communities in the aspen forest of west central Manitoba. The first year is taken from Bird ('30) and is for the year 1928. The aestival-serotinal invertebrates shown in Bird's Fig. 10 are not separated from the general mass of invertebrates. The second year is hypothetical.

5. *Layer Communities*

These are made up of smaller subordinate organisms which do not control the habitat. Many organisms are both seasonal and at the same time confined to a particular layer, *e.g.*, seasonal herbs. The stratal animals in cold climates rarely stay in the same position through the year. It is often difficult to distinguish the degree of subordination of these two types, and the same terms have been applied to them.

6. *Classification on a Physiological Basis*

The physiological suitability of organisms for certain conditions is the most important fact in determining their distribution and occurrence with other organisms. The superior suitability to a particular set of conditions and associates gives them their qualities of dominance, influence, etc. Some of these characteristics are not strictly physiological, but physiological characters are quite generally important. These physiological characters acting in connection with numerous environmental fluctuations are responsible for striking changes in abundance of many organisms and the temporary influences which they have on the communities to which they belong. The physiological responses of many organisms in brief critical periods in their life history have a surprising influence on fluctuations in abundance.

Ideally, communities may be designated and named according to their physiological characters. This would lead to their designation in general terms and would put similar communities living under similar conditions in different parts of the world into the same general category. Such a system would eliminate difficulties arising in connection with the use of taxonomic composition. Communities of totally different taxonomic composition live under similar conditions, and may be assumed to be physiologically similar. It is customary to refer to organisms which appear to be similar in their ecological relations in different parts of the world as ecologically equivalent. This is an indirect expression of the desirability of physiological designation. Again Nichols' ('23) community *type* is an expression for the similarity of communities which occupy the same conditions but are of totally different taxonomic composition. Here the plant ecologist has always been able to rely upon physiognomy (landscape aspect, *e.g.*, grassland, evergreen forest, etc.), and life form to aid him in selecting comparable types. The animal ecologist is left without these guides.

Attempts at the use of the physiological basis of the classification of communities are probably doomed to failure until our knowledge of physiology of environmental relations is a hundred times that of the present. At the beginning of his studies the writer was unduly impressed with the possibilities of classification on the physiological basis. This was due to his experience with material with which he worked. The close relationship between tiger beetle species and the various relatively minor differences in conditions brought

about by plant succession (Shelford, '07) and the details of selection of egg laying sites by species of the same group (Shelford, '11, Fig. 18) had an important influence on the writer's general viewpoint. This viewpoint, as regards the breeding condition and physiological states related thereto, was further illustrated by a study of fishes (Shelford, '11a, '11b, '11c), and a little later by the study of reactions to air conditions, in which a whole series of animals belonging to different stages of forest development, including the climax, were put through a series of experimental tests (Shelford, '13). The animals tested in this fashion fell into two groups, one group represented by very weak negative or positive reactions to temperature, dryness and air movement, and those decidedly negative to high temperature, dryness and air movement (Shelford, '29, p. 291). The former belonged to the open stages of forest development characterized by cottonwood, pine or black oak. The writer conceived the idea that the striking differences in physiological characters should be the basis of community rank and the matters of community size, extent and development (succession) were less emphasized. Later a study was conducted to determine whether common behavior characters existed among the predominants of the community (Shelford, '14). The community chosen was a rapid water animal community. The results showed two common reactions. In this case one was a selection of rock bottom and the other a strong positive reaction to current. This community was designated in very general terms as a litho-rheotactic community. The same designation would be applicable to all swift water communities regardless of taxonomic composition.

In general these were the determining factors in blocking out the modifications of the classification of communities based on development, which were presented in *Animal Communities in Temperate America* (Shelford, '13a). From the standpoint of practicability this viewpoint has to be abandoned, if for no other reason, because no experiments have been conducted on more important species of most communities. Such a system, accordingly, remains a matter of inference, and the establishment of definite criteria for communities is impracticable. The use of any such system in the study of new communities is quite impracticable. The dominants, predominants, influents and important organisms of communities, otherwise designated or designatable, are the ones whose common physiological characters should be used. The type of classification advocated above should, therefore, precede the physiological work and physiological designation. The equivalents which must be substituted in *Animal Communities* (Shelford, '13a) are indicated below. With a few exceptions these changes are not serious. It is now understood that the entire area studied belongs to the deciduous forest formation (with the possible exception of the deep parts of Lake Michigan). The grassland is subclimax to forest; at most only two climax associations can be recognized, oak-hickory to the west of the midline of Lake Michigan, and beech-maple to the east. The formation includes both developmental and

climax communities, and is now used in the sense of *extensive formation* in *Animal Communities*. Terms applicable to climax communities should be applied only to oak-hickory (westerly) and beech-maple (easterly) communities in the area (pp. 235-247).

Equivalence of terms applied to developmental communities in the nomenclature in *Animal Communities* ('13a) and at present are:

Animal communities	Present nomenclature
Formation—aquatic and grassland	= Associes
Association except as noted above	= Associes
Subformation	= Associes
Stratum	= Layer Societies or Society
Consocies	= Assembly (provisionally suggested)
Mores	= Mores

The only changes in the terms applied to climax communities are Stratum = Layer Society; Consocies = Assembly.

CHOICE OF TERMS

The scientific public has been slow to develop the concepts of populations of plants and animals. The literature indicates that these concepts, as a rule, have been incomplete. This incompleteness usually may be expressed as the emphasis of certain taxonomic groups and the omission of others. This is indicated again and again in the literature by titles, phrases and discussions involving such terms as "insect communities," "mammal associations," "fish associations," etc. The use of terms has been loose and incidental with reference to communities.

Some writers have been stressing small groups of animals, treating the assemblages of fallen logs, of hot springs, of shelf fungi, etc. They have used terms and made suggestions not generally applicable, when the largest units of geographic extent are considered.

1. *The Test of an Author's Viewpoint*

The first test to apply to an author's nomenclature is expressed by this question: did he have a definite assemblage of organisms which he described, defined and limited and to which he found it necessary to apply certain terms? The second test is indicated by the question: did he consider this assemblage in relation to other larger communities and to the natural subdivisions occurring within it? The third test is expressed by the question: was he giving thoughtful consideration to the terms he used? This involves their past usage, their relations to the terms applied to the larger and smaller units, and their appropriateness. The term "large units" here is meant to apply to the largest biotic areas of the earth's surface.

2. Terms Established by Authoritative Bodies

Following the precedent of Warming's writings, the Third International Botanical Congress at Brussels, May 14-22, 1910, adopted the word *community* to cover ecological units of every degree (Flahault and Schroter, '10, p. 24). It was used in this sense by Murray and Hjort ('12, Chap. 9) by Petersen and Jensen ('11 and later), by Shelford ('13) and many others. The German equivalent for community is understood to be *gesellschaft*. It is generally understood that *société* is the French equivalent. *Lebensgemeinschaft* is understood to be the equivalent of biotic community. Contemporaneous with Warming's publications and since 1910 the term *association* has been so loosely used, as to cover ecological units of nearly every degree, by Adams, Vestal, Cowles, Fuller, Dice and many others. This constitutes the chief difficulty in the use of *association* in the technical sense proposed by Warming and restricted by Clements. *Society* has also been used in the sense of *community*. *Biocoenosis*, which is a very desirable term, originally (Möbius, '83) applied to a climax community, has also been so loosely used that it is necessary to consider that it ordinarily has no specific meaning and carries the general force of the word *community*. This term is in common use among Russian and German animal ecologists.

The term association, as adopted by the Third International Botanical Congress, is a community of definite taxonomic composition presenting a uniform physiognomy (plants) and growing in uniform habitat conditions. The formation according to the Congress is a larger unit composed of associations. How large is the formation? Its usual size is illustrated by the grassland or the transcontinental coniferous forest of North America. The association (Climax) is then also large, for example, averaging as large as the republic of France. The dominants of the association are uniform throughout its extent. A part of a particular association's dominants are found throughout the formation; others are characteristic of the association.

Since 1910 there has been a strong tendency among American plant and animal, and English plant ecologists to distinguish between climax and developmental assemblages of associational rank, applying the term *associes* to the larger developmental communities and the term *association* to the climax. From a purely scientific viewpoint this appears to be a step in the right direction, as it makes distinctions on the basis of the dynamics of communities, recognizing the less stable and more rapidly changing ones in a different category from those whose condition varies with the larger climatic variations and cycles. The criticism is made that it is not always possible to determine whether a community is climax or developmental. Investigators usually have opinions based on evidence and to fail to make the distinction tends to suppress the evidence and deprive others of part of the fruits of the investigations.

Developments of recent years, especially in animal ecology, have led investigators to regard the formation or largest biotic area as a natural unit.

From the animal side the important large mammals which have a profound influence upon the vegetation and the habitat as a whole, such, for example, as the bison in the grassland, or the moose in the coniferous forest, range over the several associations which make up the formation and also over all the developmental stages. This gives unity to the formation and makes it the fundamental large unit of ecology. Clements, who has had unusual contact with extensive areas of vegetation not modified beyond recognition, takes the same view. This does not agree with the 1910 Congress, which made the association the unit. This older view, no doubt, grew out of the study of small areas of vegetation left by civilization and with all consideration of animals omitted.

Units smaller than the association (and assosciates) present unusual difficulties. Some are due to minor variations in the substratum, others to weather or other conditions at a critical period, which gave particular species first chance at a foothold. A single pair of terms, society and socies (developmental), has been quite generally applied to subordinate assemblages within assosciates and associations. These terms apply to *three* types of subordinate communities. For example, in a climax community one has:

1. Layer societies (predominating in certain levels).
2. Seasonal societies (characterizing certain seasons).
3. Local societies (small local assemblages of subordinate species).

Other terms are in use for very special and usually smaller units, especially of sessile organisms.

To clarify concepts, more terms for the subordinate communities indicated above could be justified. Biologists have, however, developed so little contact with biotic communities and so few concepts regarding populations that there is complaint about the meager set of terms in use.

3. Basis

The basis of knowledge for community nomenclature lies in intensive study of the dynamics of certain typical communities and a wide reconnaissance of others. This means intensive study and travel. In adopting terms, the acceptance of those used by some thorough research man with wide experience and set forth by him a general dissertation, which is widely read and generally accepted, is most promising of general results.

4. The Remedy for Disputed Usages

Demonstration of communities and community phenomena by persons using or proposing nomenclature for communities is the logical way to settle disputes. This, of course, does not necessarily result in agreement, but with the same facts in mind men rarely disagree. The demonstration of community phenomena is, however, difficult. It can only be accomplished by

field excursions. These have been but little fostered by ecological organizations. It is hoped that they will be in the future.

SUMMARY

1. Taxonomic listing fails to indicate communities because it is not quantitative.
2. The limits of communities are determined by the limits of their controlling and otherwise important organisms, while still functioning as controls (dominants, influents, etc.).
3. Except perhaps for the ocean or other very deep bodies of water, all the life of an area constitutes a major community.
4. Primary divisions based upon layers occur only in very deep waters, and the lack of investigation lends uncertainty to rankings.
5. Three independent systems of classification for communities have been developed.
 - a. Based upon the family and its guests and pests without synthesis with the larger grouping to which the family (colony) belongs developed by students of aggregations, and of ants and termites.
 - b. Based upon fresh water *habitats* and to a minor degree, *communities*, but without consideration for land climates toward which most fresh water communities are tending: developed by limnologists and hydrobiologists.
 - c. Based upon an analysis and synthesis of the largest natural units, such as grassland, desert, etc., with regard to their dynamic and developmental tendencies: developed by plant and animal synecologists.
6. The development and other dynamic features of a community should be used as a basis for classification categories.
7. Terms should be selected with due regard for precedent, usage, and approval by authoritative bodies.

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VEGETATION ON NORTH AND SOUTHERN SLOPES OF MOUNTAINS IN SOUTHWESTERN TEXAS

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As one travels through the mountains of Brewster, Jeff Davis, and Presidio counties in what is known as the Big Bend Country of southwestern Texas, it is noticeable that the north and south exposures are markedly different. Most of the trees and tall grasses grow along the north slopes of the mountains, while the south slopes are sparsely covered with short grasses and other xeric vegetation (figs. 1 and 2).



FIG. 1. A typical north slope showing dense stand of oak, *Quercus grisea*.

In a previous paper,¹ the vegetation, as well as the environmental factors under which it develops on the "flats" or mountain valleys, has been rather fully described, but no description was given of the vegetation of the mountain slopes. It is the purpose of this study to consider the environmental factors of north and south mountain slopes and their relation to the development of the cover of vegetation.

Differences in the distribution of plants and plant communities due to insolation may be found in nearly all parts of the world. According to Warm-

¹ Cottler, Harvey J. 1931. Studies in the vegetation of southwestern Texas. *Ecology*, 12: 105-155.

ing ('95) the southern slopes of mountains in Greenland have an open cover of xeric vegetation "appearing as if burnt up," although the northern slopes are covered by a dense, green, mossy carpet, interspersed with many flowering plants.

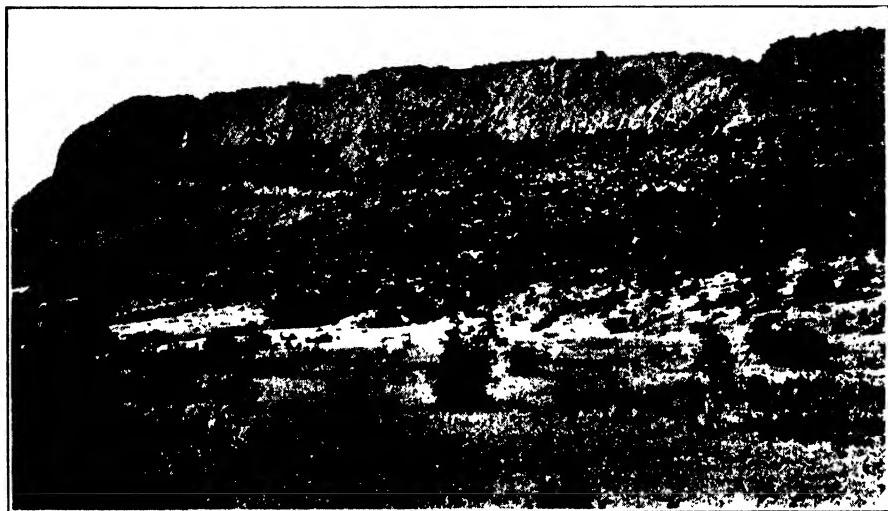


FIG. 2. A typical south slope showing the xeric vegetation. The camera was in the same position as for Fig. 1, but focused on the south slope.

Alter ('13) states that "a 5° slope to the south in southern Idaho is in the same solar climate as is a level field . . . 350 miles nearer the equator." "The northerly slopes of the mountains, [of the Great Basin Region] from which snow and rain are much more slowly evaporated, are where we find the mountain forests, while the southerly slopes, which are quickly dried in the sun after a storm, are usually covered with a ragged blanket of sagebrush, and often carry no vegetation at all."

Turesson ('14) has shown the importance of slope exposure as a factor in the distribution of *Pseudotsuga taxifolia* in the arid parts of Washington. In the drier parts of eastern Washington it "always occupies the shady northern slope of hills and ridges, and is entirely absent on the southern, thus affording a most notable example of slope exposure."

Weaver ('14), working in southeastern Washington and adjacent Idaho, found that the evaporation during the growing season was only 64 per cent as great on the northeast as the southwest slopes of the rolling hills of the Palouse prairies. A marked difference in vegetation was also reported. South slopes had on an average only 112 individual plants per square meter as compared with 200 on north slopes. Many less xeric species were almost or entirely confined to north slopes. On the buttes, the south slope was likewise covered with prairie, which the yellow pines, occupying the crests and

northerly slopes, were often gradually invading. The more sheltered, lower, north slopes were clothed with a forest of Douglas fir and tamarack. Weaver ('17) also determined that the percentage of water in the soil was constantly lower on the south slope, even at a depth of 5 feet. Soil temperature was much higher on the south slope where it also showed a wider seasonal range.

Shreve ('15) has shown that there is a close correspondence between vegetation of opposed slopes that are 1,000 vertical feet apart and that there is likewise a correspondingly close agreement between the ratios of evaporation to soil moisture. He determined ('24) the maximum temperature on two slopes of mountains in the vicinity of Tucson, Arizona, at a depth of 3 inches and at 7,000 feet altitude. The average maximum temperature over a period of 18 weeks was 13° C. higher on the south than on the north slope, and the average minimum temperature for the same period was 10.7° C. higher on the south slope. At both 8,000 and 9,000 feet altitude the seasonal mean soil temperature of the south slope was higher than that 1,000 feet lower on the north exposure. The evaporation was also found to be much higher on the south slope (Shreve, '27). He concludes that insolation is more important than air temperature in determining the temperature of the soil, and that differences between the vegetation of north and south slopes are due to a group of conditions initiated by the differences in insolation and soil temperature existing on them.

GENERAL PLANT LIFE CONDITIONS

To determine what environmental factors produced the great difference in the vegetation on the north and south slopes, a typical mountain (College Hill) was selected for investigation. This mountain has an altitude of approximately 5,000 feet. The two slopes are almost equal, being about thirty degrees, and each is covered with typical vegetation (figs. 3-4).

Water is the chief limiting factor to plant growth in this region, hence the amount and distribution of the precipitation are of great importance. The mean annual precipitation at Alpine, in Brewster county, is 14.5 inches. Most of the rainfall occurs between June and October. The showers, as a rule, are sudden and rather local. Much moisture is dissipated, moreover, in light showers that do not increase the water content of the soil. The snowfall is light and the snow usually melts within one or two days.

Practically no rain falls during March and April when temperatures are favorable to renewal of growth. This is also a season of high winds which desiccate both plants and soil. Wind movement during the remainder of the year, while relatively low, is of some ecological importance, especially on the mountain slopes.

The sunlight is intense on account of the high altitude, cloudless skies, and dry atmosphere. Clear weather is a marked characteristic of the climate. Approximately seventy-five per cent of the days are cloudless and only rarely do entirely cloudy days occur.

The winters are mild, the temperature seldom remaining below freezing during the day. Temperatures of 60° F. are common during the warmest part of the day through the winter months. Summer temperatures (in



FIG. 3. South slope of College Hill showing the vegetation and the rocky nature of the soil.

shade) of 90° to 95° are quite common and sometimes temperatures of over 100° are reached. The wide range of temperature from night to day (usually 30° but sometimes 60°) is a marked feature of the climate. The sparse cover



FIG. 4. North slope of College Hill showing the stand of oak (*Quercus grisea*) and the tall grasses.

of vegetation, low humidity, and high altitude all contribute to the intense heating of the surface soil by day and an equally rapid cooling by night, especially on the south slopes.

VEGETATION OF THE SOUTH SLOPE

The south slope is dominated by three grasses, *Bouteloua gracilis*, *B. hirsuta*, and *B. eriopoda*. These grasses do not form a dense stand. The mats and bunches are small, leaving much of the soil and rock exposed to wind and sun. Growth is very much retarded when compared with the same species on the "flats" between the mountains, their height being only about two-thirds as great, and the number of flower stalks is greatly reduced. The root systems are shallow, seldom exceeding 18 inches in depth, since the soil during the growing season is rarely wet below this level.

Only one other grass, *Heteropogon contortus*, is of ecological importance on the south slope. It is also quite common in the drainage courses where there is more available water. This grass is much taller than the Boutelouas, and grows in fairly large, dense bunches. The leaves are light green and mostly basal; the flower stalks are from 18 to 24 inches tall and are produced in abundance. The black, twisted awns are about two inches long and give the plants a very characteristic appearance. This grass is not much eaten by stock, especially when the Boutelouas are to be had. For this reason it is very noticeable, even where it is not abundant.

The most conspicuous subdominant on the south slope is *Yucca macrocarpa*. This species attains tree-like proportions, frequently a height of 10 to 12 feet and a diameter of 8 to 10 inches. The leaves are 2 to 3 feet long and 1 to 2 inches wide at the base. They taper to a very sharp point and are tough and fibrous. The dead leaves droop down along the trunk while the green ones stand erect from the crown, thus giving the plant a palm-like appearance. The flowers are born in dense panicles arising from the crown. These panicles are usually 24 to 30 inches long and 12 to 18 inches in diameter. The individual flowers are from 1 to 2 inches in width. The blossoms are produced rather early in spring, the bud stalk often appearing about the first of February. The plants are found only on the steeper slopes where the surface is very rocky (fig. 5).

Bear grass (*Nolina texana*) is another conspicuous subdominant on the south slope. The low, evergreen tufts of this grass-like plant are very conspicuous especially during the winter when the other vegetation is dormant. The individual clumps or bunches are from 18 to 20 inches in diameter; the grass-like leaves are about $\frac{1}{4}$ inch in diameter, from 2 to 3 feet in length, and are very tough and fibrous. The stem is so short that the leaves arise at the ground level. The inconspicuous flowers are born in dense panicles which seldom exceed the leaves; they are cream-colored, and about $\frac{1}{4}$ inch in diameter. The tough leaves are sometimes chewed by the cattle in winter.

when forage is scarce, but they are so fibrous that they have very little value for grazing.

At the base of the mountain where the soil is of finer texture, there are numerous *Echinocactus horizonthalonius*. This is one of the globose types



FIG. 5. *Yucca macrocarpa* on the south slope of College Hill.

of cactus commonly called the Devil's Head. It has several very coarse spines in each cluster. Large plants are from 6 to 8 inches in diameter and almost as tall, being about half buried in the soil. The blossoms are born in the crown of the plant and are about 2.5 inches in diameter. This plant has such a superficial root system that most of its absorbing is done in the upper three inches of soil.

There is a large number of other subdominants on the south slope that make their appearance during the various seasons of the year. The following are the most important:

Acacia filicioides
Anisotolotus puberulus
Asclepias nummularia
Asclepiodora decumbens

Astragalus mollissimus
Buddleia scordioides
Cassia bauhinioides
Castilleja lindheimeri

<i>Cevallia sinuata</i>	<i>Liatris punctata</i>
<i>Croton corymbulosus</i>	<i>Lithospermum linearifolium</i>
<i>Dichondra argentea</i>	<i>Mammillaria</i> sp.
<i>Dolicholus texanus</i>	<i>Opuntia</i> sp.
<i>Echinocactus wislizeni</i>	<i>Parosela aurea</i>
<i>Ephedra trifurca</i>	<i>Parosela frutescens</i>
<i>Eriogonum tenellum</i>	<i>Parosela wrightii</i>
<i>Eriogonum wrightii</i>	<i>Pentstemon acuminatus</i>
<i>Evolvulus alsinoides</i>	<i>Pentstemon jamesii</i>
<i>Evolvulus mollis</i>	<i>Podostemma lindheimeri</i>
<i>Gilia rigidula</i>	<i>Psilostrophe arachnoidea</i>
<i>Krameria glandulosa</i>	<i>Psoralcea tenuiflora</i>
<i>Krameria secundiflora</i>	<i>Sclaginella</i> sp.

VEGETATION OF THE NORTH SLOPE

The vegetation of the north slope is of a very different type except for a marked transition zone near the summit of the mountain where the vegetation of the two slopes considerably intermingle. The xeric vegetation of the south slope ranges farther down the north slope than does the more mesic vegetation of the north slope onto the xerocline. The only grass of the north slope that invades the south one to any great extent is *Bouteloua curtipendula*. None of the large, woody species of the north slope reach the summit of the mountain, but all grow far down the north slope where they are protected from the south wind and the heat of the south exposure.

The dominant grasses on the north slope are *Bouteloua curtipendula*, *Andropogon scoparius*, *A. saccharoides*, and *Sporobolus wrightii*. These grasses form a dense cover over most of the area, often so completely occupying the soil that little of the surface is exposed. The flower stalks of both *Bouteloua curtipendula* and *Andropogon scoparius* reach a height of 18 to 24 inches. These two species constitute a large percentage of the grass cover. *Andropogon saccharoides* and *Sporobolus wrightii* are more conspicuous because of their much greater height and the size of the individual bunches. The flower stalks are 36 to 48 inches high and the bunches are frequently 12 inches in diameter. However, they do not constitute so large a percentage of the cover as do the two preceding grasses.

Woody plants are quite well represented on the north slope. The most common species is an oak (*Quercus grisea*) which often grows in rather dense stands on the lower slopes and along the drainage courses. It is a very characteristic species of the mountains of the region and is quite xeric in its habit and manner of growth. The leaves are small, seldom exceeding 1.5 inches in length and .75 inch in width. They are so densely pubescent, especially on the lower surface, that the tree has a distinctly grayish appearance. The leaves are retained during the winter but are shed in the spring upon the growth of the new ones. The trunk is usually short and the

branches are numerous and more or less twisted, giving the tree a very gnarly appearance. The largest trees on the slope are about 20 feet high and 12 to 14 inches in diameter; many, however, are smaller and reach a height of only 6 to 10 feet and a diameter of 3 to 4 inches (fig. 6).

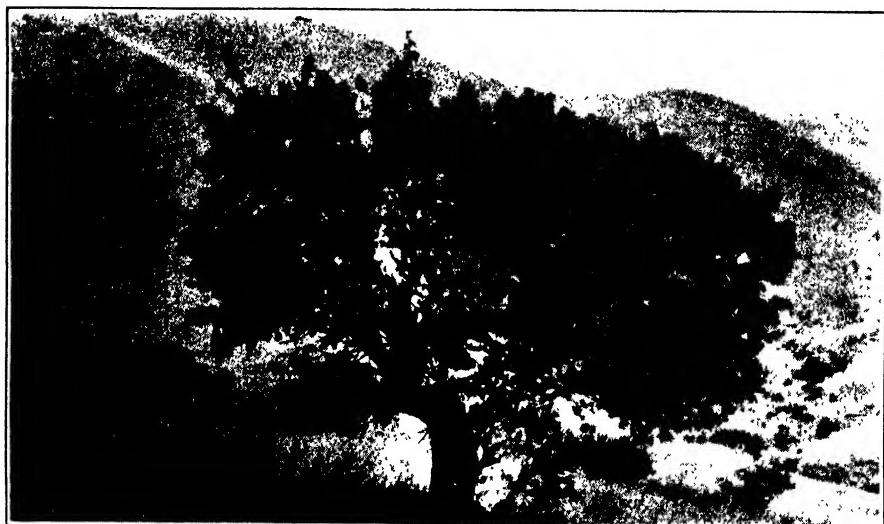


FIG. 6. An oak (*Quercus grisea*) on the north slope of College Hill.

The most common shrubs on the north slope are *Rhus virens*, *R. trilobata*, and *R. microphylla*. *R. virens* is the most conspicuous of the three as it grows more in the open. The plants are nearly prostrate and often have a lateral spread of 6 to 8 feet. The leaves are quite showy, being of a very brilliant green color, and are retained during the winter. The other two species of *Rhus* are slender, upright shrubs usually growing in the more protected locations and often under trees. These two species are deciduous and the leaves and stems are much more pubescent than those of *R. virens*.

Bouteloua gracilis and *B. hirsuta* are found on the north slope but they are distinctly subdominant and are found only near the summit of the mountain or in the most xeric locations.

The subdominants on the north slope are almost all different from those on the south slope. The most important ones are as follows:

<i>Acalypha lindheimeri</i>	<i>Eriogonum wrightii</i>
<i>Anisotolotus puberulus</i>	<i>Koeleria cristata</i>
<i>Artemisia frigida</i>	<i>Krameria glandulosa</i>
<i>Castilleja integra</i>	<i>Liatris punctata</i>
<i>Cissus incisa</i>	<i>Lichens</i> sp.
<i>Cologania longifolia</i>	<i>Menodora longiflora</i>
<i>Cologania pulchella</i>	<i>Odostemon trifoliolatus</i>

Perezia wrightii
Petalostemon candidus
Phlox nana

Solidago sp.
Ungnadia speciosa

THE ENVIRONMENTAL FACTORS

Investigations were carried on for a period of three years ('27, '28, and '29) during which time determinations of soil moisture, evaporation, humidity, and soil temperature were made approximately every two weeks during the growing season.

The stations for the study of these ecological factors were located about half way up the slope on the north and south mountain sides respectively, and in vegetation carefully selected as typical.

SOIL

The type of soil and its water content are two of the most important ecological factors in determining the distribution and growth of vegetation and must be given primary consideration in the study of plant distribution.

The soil on the two slopes is very similar in structure. Samples for water-content determinations were secured at each station at approximately two-week intervals during each growing season. Large samples of about 300 grams were taken at a depth of 12 inches. It was not thought advisable to obtain samples to a greater depth on account of the rocky nature of the soil, the lack of water penetration, and the shallowness of the root systems, especially on the south slope. In fact, most of the roots on the south slope were in the surface twelve-inches of soil. The soil samples were thoroughly dried and the per cent of moisture computed on the dry-weight basis.

The data show that during the three years the water content of the soil on the south slope was consistently lower than on the north slope. The greatest difference was more than 16 per cent and differences of 4 and 5 per cent were frequent. The seasonal average for the three years shows that the soil of the north slope contained 5.5 per cent more moisture than that of the south slope (fig. 7).

Figure 7 shows that the soil moisture on the south slope fell to a very low percentage a number of times during each growing season and especially during the season of 1927. During 1927, it was only 57 per cent as great as that on the north slope. For the other two years the percentages were 74 and 72 respectively.

No data were secured on the amount of run-off on the two slopes except in an indirect manner. It seems clear, however, that the run-off is much greater on the south mountain side. On April 26, 1927, soil samples were taken soon after a brief, heavy shower. These samples showed that the soil on the north slope contained 28.9 per cent of water while that of the south

slope had only 12.7 per cent. If the rain is of the slow, steady type, the penetration on the two slopes is about equal. This was shown by data obtained on July 29, 1928, at which time samples were taken after an extended period of gentle rainfall. The vegetation on the south slope is so sparse that

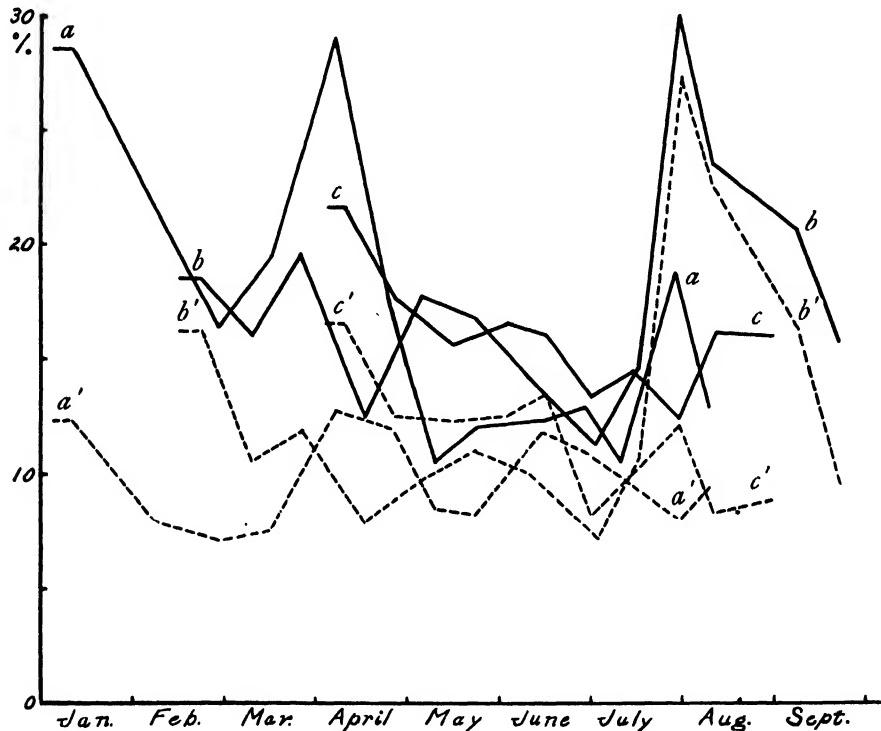


FIG. 7. Graphs showing soil moisture range throughout the season at depth of 12 inches on the north (*a*, *b*, *c*) and on the south slopes (*a'*, *b'*, *c'*) for the years 1927, 1928 and 1929 respectively.

it offers very little resistance to running water from heavy rains, which are the most common type of the region. The vegetation on the north slope, however, is dense enough to greatly retard the flow of water, thus allowing it to penetrate into the soil.

EVAPORATION

Evaporation, like water content of soil, is a very important environmental factor in plant growth and distribution, especially in a xeric region. This factor was measured on both slopes by means of Livingston's porous cup atmometers, during the three years the investigations were in progress.

The data for the three years show that during the dry part of the season the evaporation was very much higher on the south than on the north slope, but the difference on the two slopes became much less after the rainy season

began. The greatest daily difference occurred during the period from April 18 to 25, 1927, at which time the evaporation on the north slope was only 40 per cent as great as that on the south slope. No difference occurred during the period from July 17 to 21, 1929. During this time the weather was foggy and cool, a very unusual condition for the region.

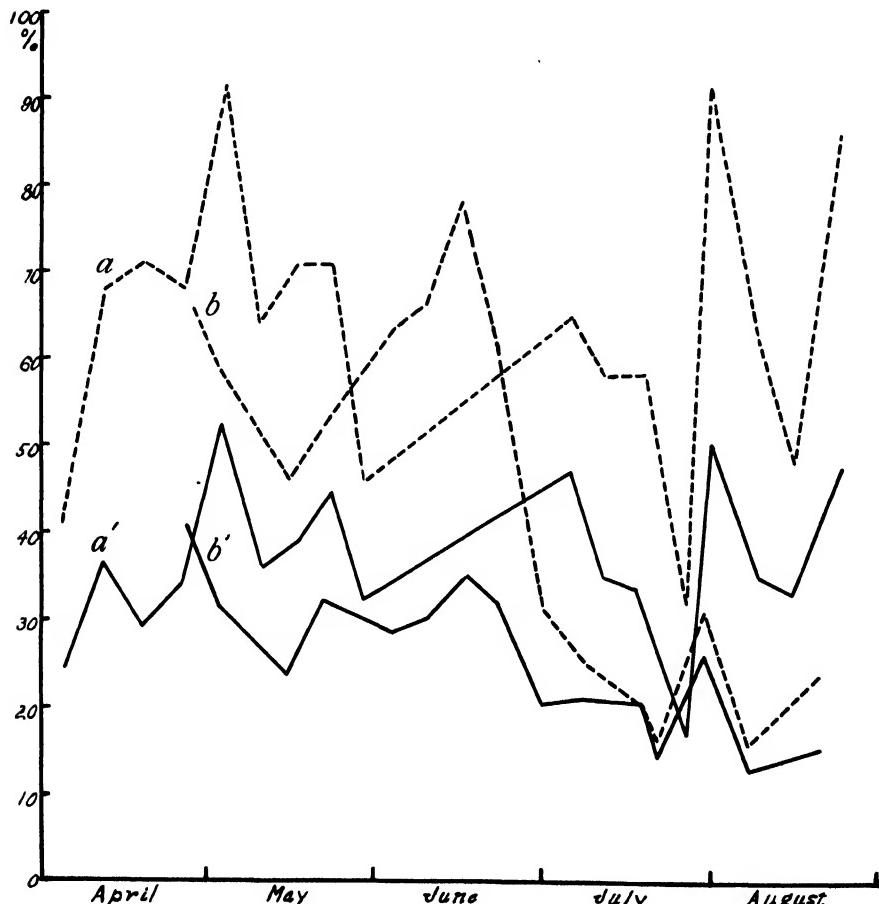


FIG. 8. Graphs showing daily evaporation rates, in cc. loss from Livingston atmometers, on the south (*a*, *b*) and on the north slopes (*a'*, *b'*) for the years 1927 and 1929 respectively.

When the whole growing season is taken into account, it is found that the evaporation during 1927 was only 56 per cent as great on the north as on the south slope. During the season of 1928, which was a wet year, the evaporation on the north slope was only 76 per cent as great as that on the south one. In 1929 the evaporation on the north slope was 62 per cent of that on the south slope (fig. 8).

The extremely xeric conditions of the south slope are very clearly shown

by the data for the year 1927. During this year the soil moisture on the south slope was only 57 per cent as great as that of the north slope, but the evaporation on the north slope during this season was only 56 per cent as great as that of the south slope.

Psychrometer readings were frequently made on the two slopes. These showed that the humidity was higher at all times on the north mountain side. The difference was usually about 5 per cent but in extreme cases 11.

No readings of wind velocity were made, though wind movement was carefully observed from time to time. The prevailing winds during the growing season are from the south and southeast and strike the south slope with all of their force, while on the north slope the wind is scarcely noticeable. Frequently the wind would be blowing almost a gale on the south slope but as soon as one passed over the crest of the mountain to the north slope the velocity was greatly reduced and when the middle of the slope was reached the wind could scarcely be noticed. This difference in wind velocity has two very definite effects. It greatly increases transpiration on the south slope and also the evaporation of moisture from the soil, much of which is exposed on account of the sparse cover of vegetation.

SOIL TEMPERATURE

Soil temperatures were determined at 2 and 12 inches in depth at the same time the soil samples were secured. With few exceptions the temperatures on the south slope were not extremely high, yet they were, as a rule, several degrees higher than those at the same depth on the north slope. A difference of 10° F. was common at the two-inch depth and in extreme cases a difference of 28° was noted. In a number of cases the temperature at 12 inches on the south slope was as high as the temperature at 2 inches on the north one. The highest temperature recorded at a depth of two inches on the south slope was 122° F., while at the same depth on the north slope the temperature was only 96°. This increase in temperature on the south slope no doubt has a markedly retarding effect on plant growth, especially when the soil moisture is reduced to a low percentage, a condition which occurs on the south slope many times during each growing season (table 1).

TABLE I. *Soil temperatures at a depth of two inches on the north and south slope*

1927	North	South	1928	North	South	1929	North	South
Jan. 10	38	62	Feb. 22	44	56	Apr. 10	68	80
Feb. 7	54	83	Mar. 9	60	92	Apr. 26	74	92
Feb. 28	62	85	Mar. 26	70	98	May 14	78	100
Mar. 30	68	86	Apr. 16	74	98	June 3	76	85
Apr. 6	88	102	May 4	68	78	June 15	74	80
Apr. 25	80	94	May 21	84	84	June 30	80	90
May 9	72	80	June 11	72	80	July 14	80	86
May 22	100	114	July 2	96	122	July 29	74	74
June 13	78	80	July 16	84	90	Aug. 11	84	94
June 27	78	80	July 29	80	82			
July 11	98	110	Aug. 19	86	100			
July 26	90	92	Sept. 8	84	96			
Aug. 9	98	120	Sept. 19	84	98			

TABLE 2. *Soil temperatures at a depth of twelve inches on the north and south slope*

1927	North	South	1928	North	South	1929	North	South
Jan. 10	38	54	Feb. 22	44	56	Apr. 10	68	80
Feb. 7	50	70	Mar. 9	56	78	Apr. 26	68	70
Feb. 28	58	70	Mar. 26	64	84	May 14	68	90
Mar. 30	60	74	Apr. 16	68	84	June 3	78	78
Apr. 6	72	84	May 4	68	75	June 15	72	80
Apr. 25	66	74	May 21	74	80	June 30	80	84
May 9	66	76	June 11	76	78	July 14	78	80
May 22	85	90	July 2	88	96	July 29	76	80
June 13	76	78	July 16	86	86	Aug. 11	80	88
June 27	78	82	July 29	72	76			
July 11	86	94	Aug. 19	76	82			
July 26	82	86	Sept. 8	74	86			
Aug. 9	88	97	Sept. 19	70	84			

The temperature at a depth of 12 inches never became extremely high on either slope but it was consistently higher on the south slope (table 2). A study of tables 1 and 2 shows very clearly that the conditions on the south slope had a much more xeric trend than on the north slope. It is also quite probable that intervals between the readings might have shown even greater differences in temperature at both depths.

VEGETATIONAL COVER

A careful study of the vegetational cover was made on the two slopes by means of both chart and clipped quadrats. The quadrats were located in typical grassy areas on dry slopes and about the same distance from the summit of the mountain.

It was found that there was approximately the same number of plants per square meter on the two slopes but those on the south side were much smaller and much less vigorous. The basal area or ground cover on the south slope was only 7 per cent but on the north side it was 14.5 per cent. Thus the basal area of the plant cover on the south slope was only 48 per cent as great as that on the north slope.

A comparison of the dry matter produced per square meter on the two slopes shows an even more striking difference. The grass on the south slope was so short that it was very difficult to find stems long enough to clip, but on the north mountain side some of the bunches of grass stood 30 to 36 inches high. The amount of dry matter produced per square meter on the south slope was only 14 grams but on the north one the yield was 276 grams per square meter. This makes the production on the south slope only 5 per cent as great as that of the north side.

The great difference in plant production on the two slopes, no doubt, is partially due to the south slope being more heavily grazed, as the better range grasses are found on this side. The grasses on the north slope are much coarser and less palatable to stock in both summer and winter. It seems

improbable, however, that the difference in grazing could alone account for such a marked difference in the production of dry matter.

SUMMARY

A study of the vegetation of the mountains of southwestern Texas shows that there is a very marked difference in the species found on the north and south slopes. Environmental conditions on the south slope are much less favorable to plant growth. Water content of soil is 5 to 16 per cent lower; evaporation is 24 to 44 per cent higher; soil temperatures are 10° to 20° F. higher at the 2-inch level, and also much higher at a depth of 12 inches. Humidity is 5 to 11 per cent lower, and wind velocity much greater.

The cover of vegetation was found to be less than one-half as great and the production of dry matter only about one-twentieth of that on the north slope. Several factors interact to produce these conditions, the water relation being the controlling one.

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PARASITES OF JAPANESE SALAMANDERS

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Japan with its great extent in latitude (22° - 50° N.) and rugged contours offers a variety of climates and habitats. The twenty species of salamanders which occur in this beautiful country (Tago, '30) are found in lowland ponds, swift mountain streams, damp forests, cultivated fields, ditches; and under logs, fallen leaves, and stones on land. Some species live permanently in water and others remain on land during most or perhaps all of the year. These animals furnished an excellent opportunity to investigate the adaptations of a particular type of vertebrate to aquatic and land life. The writer, therefore, while serving as Visiting Professor of Biology in Keiojuku University, studied the habitats, foods, and parasites of eight representative species. One species was also studied in some detail, specimens from two localities being examined during every month of the year (March 23, 1929, to February 28, 1930).

In all 362 individuals were examined. These were collected by the writer, carried into the laboratory, and studied during the day collected or on the following day. The exterior and buccal cavity were carefully scrutinized for ectoparasites. The ventral body wall was slit open a little to the right of the median line; the viscera were removed and placed on a glass plate; and the internal organs were teased apart seriatim with dissecting needles under a binocular microscope. In this way food and parasites were observed. Two temporary mounts were also made in normal salt solution of the contents of the anterior region of the intestine and the rectum and examined under a compound microscope. If there was no food present, scrapings from the wall of the intestine were examined. A slide of fresh blood from each individual also was studied for at least ten minutes if no parasites were found.

The writer is pleased to make acknowledgments to those who assisted him. Professor Katsuya Tago, who is an authority on Japanese salamanders, took many collecting trips with the writer and furnished specimens from distant localities. Professor Y. Ibara often accompanied the writer into the field and studied many of the protozoans found in the salamanders. The following persons described or identified parasites: Drs. Y. Ozaki and F. J. Holl, trematodes; Dr. H. J. Van Cleave, acanthocephalans; Dr. H. A. Baylis and Mr. J. S. Wilkie, nematodes.

HABITS AND FOODS OF THE EIGHT SPECIES OF SALAMANDERS STUDIED

The following is a list of the species studied:

Triturus pyrrhogaster (Boie). This newt is abundant throughout most of the Island of Hondo. It frequents ponds and sluggish streams. Its food consists largely of arthropods (70%), such as insects (60%), myriapods and spiders (0.6%), and small crustaceans (9%), and in all localities contains some plants (21%). Oligochaetes, snails, amphibian eggs, and fishes are also eaten to some extent. At times considerable mud or the shed skin of the salamander is found in the enteron.

Megalobatrachus japonicus (Temminck). The giant salamander frequents mountain streams in the southern part of the Island of Hondo. It is strictly aquatic. In the swift, rocky mountain streams at Komami in Gifu Prefecture when collected in September, which was the egg-laying season, salamanders had eaten crabs (86.3%), fishes (6.7%), plants (2.7%), and sandy mud (4.3%).

Tylototriton andersoni Boulenger. This peculiar, warty salamander lives in the mountains in the Loo Choo Islands of Southern Japan. The only specimen examined by the writer was shipped from the Loo Choo Islands and contained no food.

Hynobius tokyoensis Tago. This little terrestrial salamander was collected about thirty miles north of Tokyo near Fussa during the breeding season at the end of February. At other seasons it was not to be obtained because, according to the natives, it goes on land and hides in the litter on the floors of damp forests. The specimens studied came from ditches and puddles along the edges of rice fields. Their enterons contained mud (69.5%), plants (11%), insects (10.5%), and leeches (9%).

Hynobius fuscus Tago. This mountain salamander was collected from a pool near a stream at Yumoto (above Nikko) during its egg-laying season in May. Professor Tago says that it spends most of the year on the floors of moist forests. The enterons of the specimens examined contained mud (75.7%), insects (15%), plants (4.3%), leeches (3%), and myriapods (2%).

Pseudosalamandra hida Tago. This little short-tailed salamander is terrestrial, except during the breeding season. Eight specimens from Nagano were examined in April and contained no food except insects.

Pseudosalamandra stejnegeri (Dunn). This terrestrial salamander is found in the south of Japan. Ten specimens sent from Kagoshima in November contained insects (75%) and oligochaetes (25%).

Onychodactylus japonicus (Houttuyn). This long-tailed, clawed, terrestrial salamander lives among rocks along mountain streams. The larvae are often found in the streams, but the breeding habits of this salamander are unknown. The writer examined ten specimens from Hakone in May and collected ten more at Yumoto, above Nikko, in May. Food consisted of

insects (48.8%), oligochaetes (25.4%), mud and sand (17.7%), plants (6.9%), spiders (3.9%), and shrimps (2%).

The food of all the species studied consisted largely of arthropods. The observations indicate that salamanders with longer intestines ate somewhat more of vegetation than those with shorter intestines, but were too limited to permit generalizations. The variety of foods observed increased directly with the number of individuals examined. More extensive observations should therefore be made of species other than *Triturus pyrrhogaster*. The writer's records on foods are given largely because it is hoped that they may be of some value in the study of the life histories of salamander parasites. A more detailed account of the food of *Triturus pyrrhogaster* is given in the section on seasonal variations (p. 143; tables V, VII). A summary of the foods eaten by all salamanders studied is given in table I.

PARASITES

The parasites of Japanese salamanders have been studied now and then by various investigators. The following list includes all species known to the writer. Those marked with a * have been observed during the studies reported in the present paper.

**Liolope copulans* Cohn (1902)—a trematode in the intestine of *Megabatrachus japonicus*.

**Phyllodistomum patellare* (Sturges, 1902)—from the urinary bladder of *Triturus pyrrhogaster*. This species was described as *P. enterocolpium* by Holl (1930).

**Trypanosoma tritonis* Ogawa (1913)—a trypanosome in the blood of *Triturus pyrrhogaster*.

**Opisthodiscus subclavatus* (Pallas; Fukui, 1923)—a trematode in the intestine of *Triturus pyrrhogaster*.

**Acanthocephalus nanus* Van Cleave (1925)—from *Triturus pyrrhogaster*.

Lernaca cyprenacea L. (Okada, 1927)—a copepod on the skin of *Triturus pyrrhogaster*.

**Mesocoelium elongatum* Goto and Ozaki (1929)—a trematode in the intestine of *Triturus pyrrhogaster*.

Mesocoelium lanceatum Goto and Ozaki (1929)—a trematode in the intestine of *Tylototriton andersoni*.

**Mesocoelium pearsei* Goto and Ozaki (1930)—a trematode in the intestine of *Pseudosalamandra stejnegeri*.

**Mesocoelium japonicum* Goto and Ozaki (1930)—a trematode in the intestine of *Pseudosalamandra stejnegeri*.

**Capillaria filiformis* v. Linstow (Wilkie, 1930)—from the intestine of *Triturus pyrrhogaster*, *Onychodactylus japonicus*, *Pseudosalamandra stejnegeri*, and *Hynobius tokyoensis*. This parasite was embedded in the wall of the intestine.

TABLE I. Foods: summary of all species

Figures under foods indicate estimated percentages by volume. The length of intestine is given in terms of body length from tip of snout to middle of anus

**Aplectana* sp. (Wilkie, 1930)—from *Triturus pyrrhogaster*.

**Pharyngodon* sp. (Wilkie, 1930)—from *Onychodactylus japonicus*, *Pseudosalamandra stejnegeri*, and *Pseudosalamandra hida*.

*Rhabditids (Wilkie, 1930)—from *Onychodactylus japonicus* and *Hynobius fuscus*.

**Cosmocercoides tridens* Wilkie (1930)—from the intestine of *Tylopolypus andersoni*.

**Rhabdias tokyoensis* Wilkie (1930)—from the lungs of *Triturus pyrrhogaster*.

**Trichodina okajimae* Ibara (1931)—from the bladder of *Hynobius tokyoensis*.

The writer's observations on the parasites of Japanese salamanders were of course limited. More species of parasites were found in those species of salamanders in which a large number of individuals were examined, which indicates that more examinations would doubtless have yielded more species of parasites. However, the writer will probably never have an opportunity to continue such studies in the orient and those at present completed are therefore presented. The observations on one species (*Triturus pyrrhogaster*) are quite complete, as specimens were examined from several representative localities and from two localities (Samboji, Inokasira) near Tokyo during every month for an entire year.

The parasites found in Japanese salamanders by the writer are summarized in table II. It will be noticed that species of parasites are quite limited in regard to the number of species of hosts in which they occur. Intestinal flagellates, oxyurids, nematodes in the urinary bladder, and encysted nematodes (none of which were identified accurately as to species) occurred in 7, 7, 6, and 3 species of hosts, respectively. The results for other species of parasites were as follows: *Capillaria filiformis* in 4 hosts; 3 species of *Mesocoelium* in 3 hosts; *Opisthodiscus* in 2 hosts; and the following in one host—acanthocephalan cysts, *Acanthocephalus nanus*, *Rhabdias tokyoensis*, tapeworm cysts, *Phyllostomum patellare*, *Gorgoderina* sp., *Liolope copulans*, distomes encysted in the peritoneum, *Trichodina okajimae*, *Opalina* sp., *Balantidium* sp., *Trypanosoma tritonis*, and amoebas.

A careful study of the data presented in table II appears to indicate that there are on the whole fewer parasites in salamanders in the highlands than in those in the lowlands. Judged by the degree of parasitic infestation the rank of particular species in various localities is as follows: *Triturus pyrrhogaster*, Amori; *Hynobius tokyoensis*, Tanichi; *T. pyrrhogaster*, Samboji; *T. pyrrhogaster*, Akita; *Pseudosalamandra stejnegeri*, Kyu Shu; *P. stejnegeri*, Kagoshima; *T. pyrrhogaster*, Komami; *T. pyrrhogaster*, Inokasira; *Pseudosalamandra hida*, Nagano; *Megalobatrachus japonicus*, Komami; *Onychodactylus japonicus*, Yumoto; *T. pyrrhogaster*, Yumoto; *O. japonicus*, Hakone; *Hynobius fuscus*, Yumoto; and *Tylopolypus andersoni*, Loo Choo. Those at the beginning of the list have many parasites and those at the end, few. For

TABLE II. *Parasites; summary of all species*

The first figure in columns which refer to parasites shows percentage of individual hosts infested; the second the number of parasites per individual

TABLE II.—(Continued)

			No. examined	Acanthocephalus cysts	Nematode cysts	Oxyurids	Capillaria filiformis	Nematodes, bladder	Nematoctes	Rhabdias trophocensis	Cestode cysts	Thylloidoistomum	Gorgoderina	Tirolope copulans	Peritomaeal discomes	Ophthaldisca	Mesocoelium	Trichoglossa ohayamiae	Balanidium	Typhpanosoma	Flagellates, infusae	Amoebea	Total	No. of species parasites of	
<i>Megalocephalus japonicus</i> , Kōmami; June.....	356	3M 3F	6																					199	3
<i>Onychodactylus japonicus</i> , Hakone; May.....	77.9	8M 2F	10																					83.1	3
<i>O. japonicus</i> , Yumoto; June.....	67.0	8M 2F	10																					160	3.4
<i>Pseudosalamandra hida</i> , Nagano; Apr.....	71.1	8M	8																					120	6.4
<i>P. stejnegeri</i> , Kyushu; Apr.....	62.7	2M 8F	10																					188	4
<i>P. stejnegeri</i> , Kagoshima; Nov.....	49.5	4M 4F	8																					20	269
<i>Tylostomum andersoni</i> , Loo Choo; Aug.....	57.0	M	1																					100	13.3
Average.....	99.4	5.6M 3F	22	1.4 0.02	0.5 0.01	29	18.8 0.91	24.5 0.71	8.1 0.83	3.8 0.13	7.1 0.58	0.6 2.5	5.2 0.13	.05 0.01	4.0 5.2	17.1 5.2	4.4 + 0.10	28.8 1.55	9.4 5.2	77 0.10	2.0 1.0	256 1.0	6 33.9		

some reason *Hynobius tokyoensis* and *Pseudosalamandra stejnegeri* have more parasites than other species of land salamanders. The eight species of salamanders studied are compared and ranked in table III. The results show clearly that mountain species have fewer parasites than those in the lowlands. The terrestrial species have as many parasites as the aquatic species.

Protozoa showed a considerable degree of host specificity. *Trypanosoma* and *Balantidium* occurred only in *Triturus pyrrhogaster*; *Trichodina* in *Hynobius tokyoensis*; and *Opalina* and amoebas in *Pseudosalamandra stejnegeri*. Intestinal flagellates, perhaps of several species, were found in all salamanders except *Tylototriton andersoni*, of which only one long dead specimen was examined. There were about as many in aquatic as in terrestrial species.

Trematodes were more common in aquatic than in terrestrial species. *Phyllodistomum* was found only in *Triturus pyrrhogaster*; *Gorgodrina* in *Hynobius fuscus*; and amphistomes in *Triturus pyrrhogaster* and *Megalobatrachus japonicus*. Three species of *Mesocoelium* occurred in *Triturus pyrrhogaster*, *Hynobius fuscus*, and *Pseudosalamandra stejnegeri*. *Liolope* was found only in *Megalobatrachus japonicus*, and another distome was found encysted in *Triturus pyrrhogaster*. Except for the genus *Mesocoelium* there were more trematodes in aquatic species than in terrestrial species.

Encysted cestodes were found in *Pseudosalamandra stejnegeri* from two different localities, but no tapeworms occurred in other salamanders.

Nematodes were found in several species of salamanders. *Rhabdias* occurred only in *Triturus pyrrhogaster*. Bladder nematodes and oxyurids were more often encountered in land than in aquatic salamanders, but *Capillaria*, which was found in four species of hosts, was usually more abundant in newts (*Triturus pyrrhogaster*) than in terrestrial salamanders. Encysted nematodes were found in three species of hosts.

Acanthocephalans (*Acanthocephalus nanus*) were found only in *Triturus pyrrhogaster* near Tokyo, except for some found in an escaped *Megalobatrachus japonicus* which was captured in a canal in the city of Tokyo. Encysted acanthocephalans also occurred only in newts near Tokyo.

Certain types of parasites were found only in aquatic salamanders: i.e., *Trypanosoma*, *Balantidium*, *Phyllodistomum*, amphistomes, distomes,

TABLE III. Rank of species of salamanders as regards degree of infestation with parasites.
In columns the rank comes before the figure which gives degree of infestation

Species	Ave. total % of infestation	Ave. total no. of parasites	No. of species, parasites	Average rank
<i>Triturus pyrrhogaster</i>	1: 338	5: 10.4	1: 13	2.3
<i>Pseudosalamandra stejnegeri</i>	2: 321	4: 33.7	2: 8	2.7
<i>Hynobius tokyoensis</i>	3: 290	3: 35.5	3: 7	3.0
<i>Pseudosalamandra hida</i>	5: 188	1: 269	4: 4	3.1
<i>Megalobatrachus japonicus</i>	4: 199	2: 83.1	6: 3	4.0
<i>Onychodactylus japonicus</i>	6: 140	6: 3.9	5: 4	5.7
<i>Hynobius fuscus</i>	7: 110	7: 2.27	7: 3	7.0
<i>Tylototriton andersoni</i>	8: 10	8: 1.0	8: 1	8.0

Rhabdias, and acanthocephalans. Others occurred only in terrestrial hosts: *Opalina*, amoebas, *Trichodina*, *Gorgoderina*, and cestode cysts. Intestinal flagellates, *Mesocoelium*, *Capillaria*, nematode cysts, bladder nematodes, and oxyurids were present in both aquatic and terrestrial hosts. The last two types were more abundant in the latter. The occurrence of parasites such as are discussed in this paper is probably associated as much with host specificity, intermediate hosts, and other biotic factors as with particular localities or habitats.

SEASONAL VARIATION IN THE PARASITES OF THE JAPANESE NEWT

Two localities near Tokyo were selected for the study of the parasites of the Japanese newt, *Triturus pyrrhogaster* (Boie), at all seasons of the year. These were about four miles apart. Samboji Pond, near the village of Sakujii, was small, about a quarter of a mile long, and shallow, being nowhere deeper than three to four feet. Inokasira Pond, at Kichijoji, was larger (half mile long), deeper (10 to 15 feet), surrounded by a grove of Cryptomeria trees and fed by strong-flowing springs. It was surrounded by a public park which contained a temple. Largely on account of its greater volume the water in Inokasira Pond was cooler in summer and warmer in winter than that in Samboji Pond. For example, on February 25, 1930, the temperature six inches below the surface at 9:20 A.M. at the outlet of Samboji was 13° C.; on the same day at 11:00 A.M. at the outlet of Inokasira the temperature six inches below the surface was 15.4° C. The newts in Samboji were somewhat smaller than those in Inokasira; the average lengths being 53.2 mm. and 57.6 mm., respectively. Newts were collected on about the twenty-fifth day of each month from both the ponds. Careful records were kept of both foods and parasites. These are summarized in tables IV to VII.

The foods (tables V, VII) eaten by the salamanders did not differ much in the two ponds. In Samboji more crustaceans (35.1%), oligochaetes (7.6%), snails (4.2%), and plants (15.0%) were consumed; in Inokasira more of vertebrates (14.7%), insects (30.5%), and mud (15.7%). The food in the latter pond was probably a little more nutritious. Perhaps this, with the less variable temperature, was responsible for the larger size of the newts in this pond. On the whole more insects were eaten in summer and more crustaceans in winter.

Considering the percentage of newt hosts infested with parasites (tables IV, VI), there was some variation throughout the year. In Samboji more newts were infested with *Trypanosoma*, *Balantidium*, *Mesocoelium*, encysted peritoneal distomes, *Rhabdias*, *Capillaria*, nematode cysts, acanthocephalans, and acanthocephalan cysts. In Inokasira more newts were infested with intestinal flagellates, *Opisthodiscus*, and *Phyllobothrium*. The latter pond has a slightly lower average total percentage of infestation (329:322).

TABLE IV. Parasites of *Trichurus pyrrhogaster* in Samboji Pond; March 23, 1929, to February 25, 1930
 Under parasites the first figure shows percentage of newts infested and the second indicates average number of parasites per individual

Month	Length, mm.	Sex	Typefauna												Total
			Cysts, nematode	Oxyurids	Rhabditas	Capillaria	Diptera, Dipteronemal	Phyllocladida	Mesocotilium	Optistodiscus	Balaenidium	Typhlosoma	Insectimorphs		
January.....	50.9	8M 1F	13 .13	75 8.8	50 1.0	13 .13	13 .13	25 .25	25 .88	63 50	100 100	427 11.3			
February.....	55.2	7M 3F	10 .1	20 3.1	20 1.3	10 .1	10 .1	30 .4	10 .1	70 80	100 100	360 5.2			
March.....	54.5	9M 1F	10 .2	10 .	70 .	20 .9	20 .5	40 .4	10 .1	30 2.5	70 60	80 70	390 4.6		
April.....	54.9	7M 3F	10 1.1	20 .1	10 5.3	70 5.0	20 .	10 .	10 .1	10 .	60 .	60 .	310 11.7		
May.....	51.5	8M 2F	10 .	10 .	60 1.1	30 1.3	20 .2	10 .1	10 .	60 .	50 .	80 .	320 3.6		
June.....	51.8	9M 1F	10 .	10 .2	70 2.1	30 1.9	20 .5	20 .	30 1.4	100 .	90 .	450 6.3			

TABLE IV.—(Continued)

Month	Sex	Length, mm.	No. examined	Acanthoccephalus cytels	Acanthoccephala nematode	Oxyurids	Capillaria	Rhabditas	Phyllodistomum	Mesocotilium	Bulatridium	Tyypanosoma	Intestinal helminths	Total	
July	54.8	3M 10 7F	10	.1	50 2.1	.8		.1	10 .1	20 .2		60	60	80	320 3.3
August	52.6	10M	10		40	1.0			10 .1		10 .2	20	30	30	140 1.3
September	53.8	6M 4F	10		20	.3	30 .5	1.7			10 .4	10	50	40	70 280 3.3
October	50.9	5M 5F	10	.7	10	.1	20 .5	.3	10 .1	20 .2	10 .1	60	80	90	320 2.0
November	54.5	7M 3F	10	.1	20 .8	.8	50 2.8	.6			40 .7	10 .1	30 1.5	70	60 80 6.6
December	53.4	10M	10		20	.3	30 .5	1.2	60		10 .1			30	70 50 2.1
Average	53.2	7.4M 2.4F	9.8	2.5 0.10	6.9 0.19	17.9 1.31	1.7 0.33	46.7 1.47	16.9 0.98	0.8 0.15	16.9 0.23	12.9 0.15	13.8 0.66	58.6 60.0	75.8 5.66
														331	331 5.11

If the number of parasites per individual is compared in the two ponds the differences are more striking. Samboji again leads in *Mesocoelium*, encysted distomes, *Rhabdias*, *Capillaria*, nematode cysts, acanthocephalans, and acanthocephalan cysts; Inokasira in *Opisthodiscus* and *Phyllodistomum*. The average number of parasites, however, is much greater in Samboji (5.11) than

TABLE V. *Food of Triturus pyrrhogaster in Samboji Pond*
The figures represent percentage by volume

Month	Own skin	Fishes	Insect, adults	Insect larvae and pupae	Insect eggs	Shrimps	Isopods	Amphipods	Entomostraca	Oligochaetes	Snails	Plants	Algae	Seeds	Mud	Unknown
January ..			5.0	3.1		28.1	38.5				4.0	7.5	2.1		11.9	3.8
February ..		9.7		25.6		5.4	13.1	6.0				3.4	14.8	1.5	16.5	
April.....				25.0		51.4						22.6		1.0		
May.....	6.0	42.5	1.2	1.0	11.0	15.3					4.0	18.5		.5		
June.....		15.0	32.0								2.5	.6				
July.....	1.0	3.5	14.5	17.5	6.0	22.5		1.0	46.2	2.0	6.0	4.0				
August	1.7		7.2	15.5		41.7			0.1	16.5	2.8	11.7		1.1	1.7	3.7
September ..	3.0	8.9	17.2	4.4		11.7				18.9		19.2	3.3	10.0	3.3	6.0
October ..	10.0		19.5	2.0		24.0	30.0				4.0	10.0				.5
November ..			1.1	2.7		25.0	30.0				12.6	4.4	7.8		5.6	10.6
December ..	2.0			10.5		12.0	19.5				10.0	10.0	6.5	4.5	25.0	
Average ..	1.6	2.3	11.3	12.7	0.6	21.2	13.3	0.6	+	7.6	4.2	10.2	3.1	1.7	7.1	2.2

in Inokasira (4.6). Perhaps these facts are significant in connection with the larger size of the newts in Inokasira.

Seasonal variations are marked in some types of parasites and are practically absent in others. In Samboji, the percentage of infestation with all types of protozoans decreased to 30 per cent or less in August and that with trypanosomes rose to 100 per cent only in winter. In Inokasira, *Balantidium* infestation decreased greatly in August and trypanosomes were completely absent in October and December. Amphistomes were never abundant. *Mesocoelium* was more common and varied in a more or less erratic way. *Phyllodistomum* was somewhat less numerous and also erratic in seasonal distribution. Nematode cysts were more numerous during cold weather in Inokasira but were also numerous in July in Samboji. *Rhabdias* and *Capillaria* in both ponds were most abundant in spring. Oxyuroids were uncommon and erratic. Acanthocephalans were most prevalent in both ponds during the cold months. The fact that nematode cysts and acanthocephalans were most often observed during cold weather agrees with the finding of more nematode cysts (table II) at Akita (100: 17.0) and Amori (90: 16.0), which are in the northern part of Hondo, whereas fewer were found at southern stations. The writer ('24, p. 166-167) in studying the yellow perch in Wisconsin lakes found that acanthocephalans were most numerous in

TABLE VI. *Parasites of Triturus pyrrhogaster in Inokasira Pond; March 23, 1929, to February 25, 1930*

Under parasites the first figure shows percentage of newts infested and the second indicates average number of parasites per individual

Month	Length mm	Sex	No. examined	Cystoids, nematoide			Capillaria			Rhabditidae			Phylloidae			Ophisthodiscus			Mesocotium			Balanidium			Trypannosoma			Intestinal flagellates			Total		
				Acanthocephala	Cysts, nematoide	Oxyurids	Ciliata	Gastronemes	Amphipoda	Cladocera	Crustacea	Nematoda	Monogenea	Leucostomatidae	Leptostomatidae	Trichostomatidae	Trichomyctidae	Trichomycteroidea	Trichomycteroidea	Trichomycteroidea	Trichomycteroidea	Trichomycteroidea	Trichomycteroidea										
January . . .	56.9	9M	9				22	.22		44	1.7	56	1.8				45				89					256	3.7						
February . . .	64.9	5M 5F	10				30	1.1		20	.3						40	2.1	.9		40					60		240	4.4				
March	57.1	7M 3F	10							20	.2						50	2.0	.1		50					100		330	2.3				
April	55.7	5M 4F	10							70	20						60	1.0	.1		80					90		430	5.7				
May	48.0	8M 2F	10								1.4	2.0	1.9	.1			90	3.7	.8	.5	10	20	60	90		100		430	7.0				
June	54.0	6M 4F	10														60	1.0	1.3	.8	10	10	60	80		90		380	5.1				

TABLE VI.—(Continued)

Month	Length sex	No. examined	Acanthocephalia	Cysts, nematode	Oxyurids	Capillaria	Rhabditias	Phyllodistis column	Mesocotium	Balanustidium	Trypanosoma	Intestinal flagellates	Total		
July	60.9	3M 7F	10	60 2.0		60 1.7			10 .2	60	80	100	370	3.9	
August	59.4	2M 8F	10	10 .2		40 .8	10 .2	70 .8	10 .1	30	90	70	340	2.2	
September . . .	57.3	6M 4F	10	30 .6		20 .4		30 2.1	20 .3	50	40	100	290	3.4	
October	61.9	4M 6F	10	30 .8		50 .5		10 .8.	40 .7	50		70	250	2.8	
November . . .	56.5	4M 6F	10	10 .1		60 .1	20 .2	.5	10 1.2	.1	30 4.0	40	70	360	8.3
December . . .	58.7	9M	9	33 5.78						22 .44		33	89	197	6.9
Average	57.6	5.8M 4.0F	9.8	0.8 0.01	16.9 0.91	0.8 0.01	46.0 1.19	7.5 0.36	36.2 1.20	17.3 0.39	8.5 0.53	52.3	50.0	85.7	323 4.6

TABLE VII. *Food of Triturus pyrrhogaster in Inokasira Pond*
The figures represent percentage by volume

Month	Own skin	Toad eggs	Fishes	Insects, adult	Insect larvae	Spiders	Shrimps	Isopods	Amphipods	Entomostreaca	Oligochaetes	Leech cocoons	Smalls	Plants	Algae	Seeds (Rice)	Mud	Unknown	
January.....	12.0	8.5	1.0	15.8	37.2	.5	12.4	2.8	.3	.6	4.4	2.5	1.7	1.1	22.8				
February.....				1.0	10.5	6.3	29.8	3.5					5.0	5.0	25.4				
April.....				26.2	10.0	10.0	3.8						38.8	11.1	43.1				
May.....				24.5	13.5	24.5	1.0	9.5		10.0			37.0	12.5	10.5	9.4			
June.....				63.6	7.7	9.7							1.0	3.0	6.9	8.8	2.5		
July.....				2.5	8.1	18.1		30.0					.6	10.0	2.6	2.5	14.4		
August.....				13.8	5.6	39.3	34.4	.2	6.1				1.7	3.9	+	.3	1.1		
September.....				.6	2.6	10.0	15.6		62.8	.6				2.5	9.5		32.5		
October.....				.6	6.7	10.0	15.0		9.5	21.0				36.0	5.0	4.5		13.8	
November.....				13.6	5.9	5.8	15.4												
Average.....	4.0	0.8	9.9	12.5	17.0	1.0	0.1	18.1	3.0	+	1.0	0.2	0.1	1.9	6.2	7.0	0.3	15.7	1.2

spring and that certain nematodes became abundant in autumn and winter. In the case of *Triturus pyrrhogaster* the seasonal increase of nematoid worms may follow and be associated with the increase of insect and crustacean foods during the summer and autumn months.

DISCUSSION AND CONCLUSIONS

The habits, foods, and parasites of eight species of Japanese salamanders were studied. Terrestrial species of salamanders were found to have about as many parasites as aquatic species. Many parasites were found in only a single species of host and host-specificity is perhaps as important a factor in the occurrence of parasites as general habitat. On this account the fact that certain species of parasites were found only in aquatic or terrestrial hosts is of little significance. The many factors which control the distribution and occurrence of salamander parasites are complex and at present confusing. They are probably concerned with skins, foods, and adaptations to particular types of foods (such as length of enteron, secretions, epithelia, etc.), intermediate hosts, and other factors.

Salamanders which live always in water are not on the whole very different from those which dwell continually on land. Three species of European salamanders (*Triturus*) can apparently smell as well in water as on land. When such animals are changed from one medium to the other the olfactory organs require three or four days to become adjusted, but soon function as well as before the change (Matthes, '24). Hegner ('29), in studying the American newt, *Triturus viridescens* (Rafinesque), which spends part of its life on land and part in water, found that both aquatic (100%) and terrestrial (93%) newts contained intestinal flagellates, but that aquatic newts (60%) had trypanosomes in their blood and terrestrial newts had none. The writer in the studies described in the present paper has found no especially significant differences between the parasites of aquatic and terrestrial salamanders in Japan. Acanthocephalans and most trematodes were found only in aquatic salamanders; nematodes were erratic in distribution; protozoans, except intestinal flagellates, were confined to single host species. Trematodes and acanthocephalans are probably confined largely and wholly, respectively, to aquatic habitats by their dependence on particular intermediate hosts. The writer found fewer parasites in salamanders in the mountains than in those in the lowlands. He found no parasitic copepods on salamanders, as Okada ('27) has done.

The foods and parasites of the newts in two Japanese ponds were carefully compared during every month for an entire year. The ponds were not far apart (4 miles). One of them (Samboji) was shallow, small, muddy, and variable in temperature; the other (Inokasira) was larger, deeper, and less variable in temperature. The newts in Samboji were smaller in size; ate more of crustaceans, oligochaetes, snails, and plants; and had more para-

sites. Those in Inokasira were larger; ate more of vertebrates, insects, and mud; and had fewer parasites. In both ponds there were seasonal variations in parasites and foods. In New England Miss Morgan ('30) found that newts ate least in spring. This was apparently not true of the newts near Tokyo, which contained food at all seasons. Lung nematodes (*Rhabdias*) were most abundant in spring; acanthocephalans and nematode cysts in winter. Nematode cysts and acanthocephalans were also found to be more abundant at northern than at southern localities in Japan (table II). These parasites apparently do best at low temperatures. In yellow perch in Wisconsin lakes the writer ('24) found that acanthocephalans reached their maximum in spring and were more abundant in shallow waters than in deep, cool waters. In Japanese newts protozoan infestations showed the lowest percentage in August in Samboji, but were infrequent in Inokasira.

On the whole the observations reported in this paper do not show striking differences between the parasites of aquatic and terrestrial salamanders. Certain types of foods and parasites are more often found in species which are characteristic of land or water, but in general these are similar in the two groups of salamanders.

SUMMARY

The habits, foods, and parasites of eight species were studied. Many parasites were found in only a single species of host, and host-specificity is believed perhaps to be as important a factor in determining the occurrence of parasites as habitat. Some types of parasites were found only in aquatic and others only in terrestrial salamanders, but on the whole there was little difference between the two. The newts in two ponds were examined each month for an entire year. Significant correlations were found between body size and foods, parasitic infestation, and other environmental conditions. Some parasites showed seasonal variations in abundance. There were fewer parasites in mountain salamanders than in those in the lowlands.

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THE MORPHOLOGY, PHYSIOLOGY AND ECOLOGY OF *COLDENIA CANESCENS*

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INTRODUCTION

The smaller plants of mesic habitats may usually be classed either as shrubs or as herbs, with a bare sprinkling that do not fall conveniently into either category and have been termed by some as half-shrubs. Such a division is more a convenience than a necessity in a mesic climate, but in the drier conditions of the desert or semi-desert there is a moderately large group of plants which fall readily within this class and cannot correctly be termed either herbs or shrubs.

This habit is of the first importance in utilization of the none too plentiful water supply, which is often available for only a few hours following a summer shower. Coupled with the permanent root system, plants of this type often have the ability to shed part or all of their leaves and herbaceous stems during the long dry intervals, in this way reducing water loss to a minimum, and at the same time being ready quickly to put forth new leaves. *Coldenia canescens* DC. is a plant of this type that occurs rather plentifully on the lower bajadas of the mountains around Tucson, Arizona. I have never seen the plant in the washes or on the upper bajadas or summits near any of the localities where it is common.

Coldenia is described by Jepson ('25) as follows: "Stems gnarled, woody or rough barked, prostrate or procumbent from a stout perennial base, herbage tomentose and hispid, leaves ovate to oblong, entire." The plant even at the end of the spring growing season is rarely as much as one decimeter high but may spread out to slightly more than that width. Many of the leaves and a fair portion of the young branches do not remain alive from one year to the next, but dry up, usually after the end of the summer rainy season. They are retained by the plant, however, for some time, making it appear as though it were in full leaf throughout the year. This deception is increased by the dense hair covering which gives the whole plant a grayish appearance both when dead and alive.

This study includes only the grosser morphological features of the plant and attempts to correlate them where possible with its ability to live under arid conditions.¹

¹ I wish to thank Dr. Forrest Shreve for his suggestions during the course of the work.

MORPHOLOGY

Stem

There is a very definite central pith present, which is triangular in cross section, with the sides of the triangle incurved and the corners rounded. These central pith cells have intercellular spaces which merge in and near the center to form one or more chambers resembling to a certain extent the lacunae of hydrophytes.

The cells of the primary xylem are small and few in number, passing almost at once into the secondary xylem. These are larger and often heavily lignified. Tracheae and wood fibers are the only cell types observable, and these are present to approximately the same extent.

Definite annual rings are formed, so that in the main stem of an old plant I was able to count 15 rings which probably represent that many years of growth.

The phloem is primary for the most part and grades off into the pericycle with no definite demarcation between.

Viewed transversely the cortex outside of the pericycle is seen to be only 1-3 cells thick while the individual cells are larger than those of the pericycle. In the young plants the cortex extends unbroken to the epidermis, which is composed of small non-cutinized cells a single layer in thickness. In the older stems a definite cork is formed while immediately inside of this region a band of cortical cells encircling the stem becomes filled with tannin. Outside of these lies a fairly thick layer of periderm, divided unequally into a comparatively small amount of phellogen and a large amount of phellem. The epidermis of the two year old stems is largely sloughed off except for the hairs, many of which remain.

The hairs present on the stem are all of a single type; multicellular with an enlarged base and are somewhat filiform in general shape. No stomata were observed on the stems.

Leaf

The leaves are strongly revolute and average about a centimeter in length and only slightly less in width. . .

The upper epidermal cells are round to rectangular except for the cells serving as hair bases. These are somewhat elongate and filled with a granular appearing mass. The hairs sometimes appear branched, but in these cases it is not a true branching since two epidermal cells lying side by side each gives rise to one hair. These setiform hairs are interspersed with an occasional short, very heavy, usually two-celled type that gives the leaf its hispid character. These may be present on either the upper or the lower surfaces.

On casual examination of the leaf in cross-section, the most noticeable feature is the large amount of palisade tissue as compared with sponge. As this condition is common among xerophytes it is not surprising to find it

occurring here. In the leaves observed, the palisade tissue contained three to five layers while the sponge was either lacking entirely, except around the veins, or was limited to 1-4 cells in thickness. The usual condition seems to be a single layer of palisade tissue, occupying about $\frac{1}{3}$ the thickness of the leaf, the individual cells of which are 8-12 times as long as wide. These abut upon the sponge when it is present, or when it is not, upon more palisade cells. The sponge may occupy $\frac{1}{15}$ the total leaf thickness. The lower palisade parenchyma is 2-4 cells thick and comprises altogether about one-half the diameter of the leaf, with the individual cells about ten times as long as wide. Chloroplasts are rather evenly distributed throughout the whole parenchyma. In the older leaves an occasional palisade cell is filled with an opaque mass much resembling tannin.

Intercellular spaces in the leaf are practically lacking except immediately in connection with the stomata, and even here they are small. As will be seen later, the plant has a large total external leaf surface, but as is evident from an internal examination a relatively small true transpiring surface, since transpiration takes place largely from the cell walls which are exposed to the intercellular spaces in the leaf interior, rather than from the epidermis.

The lower epidermal cells are slightly smaller than the upper and are more thickly covered with hairs, which are of the same types as those described for the upper surface.

As would be expected from the nature of the leaf, stomata are limited to the abaxial leaf surface. These are not sunken nor in any way protected to prevent excessive transpiration, but are on the contrary slightly raised above the plane of the leaf surface. An attempt was made to gain some idea of stomatal frequency but this was rendered almost impossible by the dense mat of hairs clothing the leaf. They are not numerous, however, since the cross-section of a leaf cut 10 microns thick rarely revealed more than 2 or 3, while often none were visible.

Root

The root system, like that of the majority of desert perennials is large in comparison with the size of the crown of the plant. The roots are so brittle that it was impossible to excavate any of the systems intact. One typical plant was dug out and the course of the various roots charted (fig. 1). Both horizontal and vertical roots are present, thus enabling the plant to absorb moisture from either light showers or the more permanent water from lower depths. The horizontal roots extended a maximum distance of 53 centimeters from the plant at an average depth of only 5 centimeters from the surface. The tap root extended vertically to a depth of 22 centimeters with almost no branching except at a point about 5 centimeters from the surface where the majority of the lateral branches originated. The secondary roots also were almost without branches.

The internal anatomy of the mature root in no way differs from that of a typical woody plant. The xylem occupies about one-half the total diameter. The cells of the cortex are firm and almost without air spaces while a comparatively heavy layer of bark is present. This was so filled with an almost opaque substance that the structure of the cells could not be made out.

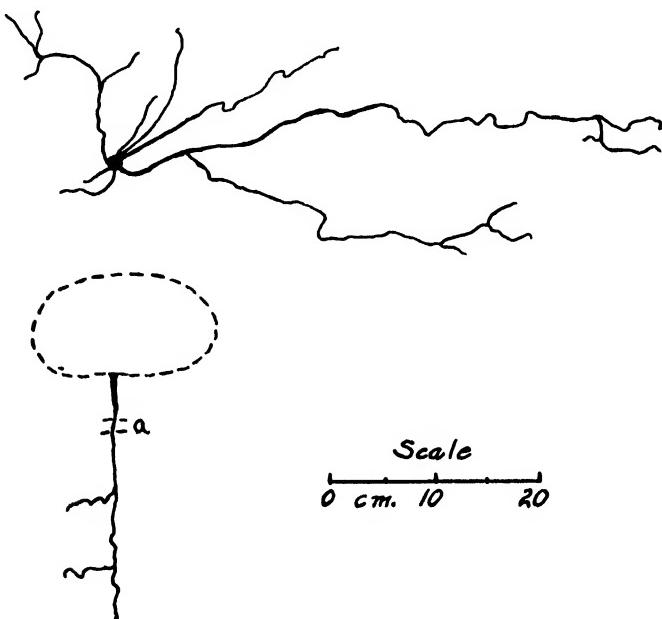


FIG. 1. Vertical and horizontal distribution of the root system of a single plant of *Coldenia canescens*. Point of origin of majority of lateral roots is indicated at *a* on the sketch of the vertical system.

PHYSIOLOGY

Osmotic Values of Cell Sap

Leaf samples were collected from fen plants, from which five determinations were made of the osmotic values of the expressed saps. The values were determined by the freezing point method with the Drucker-Burian thermometer as described by Gortner and Harris ('14) and by Walter ('31). Two readings of each sap sample were taken and these averaged to give a more accurate determination. The results are given in table I.

The osmotic values here obtained are low as compared with those of extreme xerophytes and fall into the upper range of values for typical mesophytes. It is unlikely that this value is high enough to assist sensibly in cutting down transpiration loss. It must be borne in mind, however, that these readings were made from material gathered at a time when the plants

TABLE I. *Osmotic values of cell sap in atmospheres*

Plant no.	1st determination	2nd determination	Average	Total average
1	17.68	18.04	17.86	
2	19.24	19.96	19.60	
3	22.72	23.44	23.08	
4	18.65	19.48	19.06	
5	23.36	23.32	23.34	20.59

were undergoing their most rapid growth and the water content of the soil was high enough to support a crop of annuals which are quite mesic in habit. A similar series of determinations made from material gathered toward the close of the fall dry season would undoubtedly yield considerably higher values.

Water Content of Crown

A series of eight plants was used to determine the amount of water present in the above ground portion of the plant at the time of maximum growth, which gave the following results (table II).

TABLE II. *Water content of plants*

Plant no.....	1	2	3	4	5	6	7	8	Average
% Water.....	9.2	15.5	20.9	6.5	7.6	15.3	14.9	11.5	12.7

A determination made at the same time of the amount of water present in the leaves and young twigs of *Populus macdougalii* Rose gave a result of 18.5 per cent. As nearly as possible the same comparative amounts of leaf and stem were used in both *Coldenia* and *Populus*.

The water content of the plant is seen to be low as compared with a typical woody mesophyte even at its optimum period of growth. While a constant low water content may serve to lessen the total water requirement of non-succulent plants, it is by no means so efficacious a method of drought protection as that possessed by the cacti and a few other desert perennials that have the ability to store water moisture in some part of the plant during periods of excess. The evolutionary trend in non-succulents seems to have been toward reduction rather than increase of parenchyma.

CONCLUSIONS

Drought resistance among plants may be due to a single characteristic or, as is more often the case, to a combination of them. *Coldenia canescens* is typical of this latter type since it possesses the following structural or physiologic modifications which tend to cut down the water loss or increase the intake: The presence of hairs; osmotic pressure above that of the average mesic leaf; revolute leaf edges; reduced number of stomata per unit area;

large amount of palisade tissue with little intercellular space within the leaf; death of a portion of the leaves during drought; a root system that enables it to derive water from superficial as well as deeper moisture supply; and an extensive root system.

While the total leaf surface is large, the total transpiring surface is small, and the food manufacturing area is not decreased in spite of the reduction of transpiratory surface. At the same time the dense covering of hair protects the chlorenchyma from excessive light.

SUMMARY

As is to be expected, internal root and stem structure of *Coldenia canescens*, as typical of desert perennials of the half shrub type, does not differ noticeably from more mesic plants of the same type. The features characterizing the leaf of this plant lie principally in the formation of palisade instead of sponge parenchyma and in a probable reduction in the number of stomata per unit area.

The root system is composed of both horizontal and vertical branches enabling the plant to utilize all available water. Branch roots are few and when they do occur are usually comparatively large.

Internally the roots do not differ markedly from typical roots.

The average osmotic sap value for ten plants was 20.59 atmospheres.

The amount of water from eight plants varied from 9.7 parts per 100 of dry weight to 20.9.

The total leaf surface is large, ranging in the two plants measured from 27,166 to 33,718 sq. mm.

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THE INFLUENCE OF CONTINUED HEAVY GRAZING AND OF PROMISCUOUS BURNING ON SPRING-FALL RANGES IN UTAH

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Since approximately eighty-five per cent of the gross area of about fifty-two million acres of land in Utah is now utilized for grazing purposes¹ the production of livestock is a very important phase of agriculture in the state. Because of a dry climate, a short growing season, rough topography or insufficient water for irrigation, but little more than twice the present area of about two and one-half million acres of farm land in Utah will ever be cultivated under present known methods of agriculture. Hence the economic welfare of the state depends to a great extent upon keeping the grazing lands fully productive.

The aim of the present study has been to determine the changes which have taken place in the character of the vegetation and the grazing capacity on the foothill area or the so-called spring-fall range type of Utah as the result of grazing, fire or other humanly induced factors, during the four score years that the region has been settled. This study is part of a research project recently undertaken by the Intermountain Forest and Range Experiment Station of the Forest Service, to develop more suitable methods of range management for this important class of grazing land.

Range livestock are either grazed on the semi-desert lands or fed on farms and ranches during the winter and, for the most part, are grazed in the high mountains during the summer. From approximately the middle of April until the latter part of June each year, after the animals cease to do well on the semi-desert range or in the feed lot and before the vegetation on the high mountain range has made sufficient growth to be grazed, the cattle and sheep are turned on to the lower mountain slopes and adjacent foothills. They are returned to this range again for a period of a month to six weeks in the fall. Climatic conditions as influenced by topography limit the area of spring-fall range. The available area has been reduced by farming and that left has been heavily overgrazed, and in places, further damaged by fire until there now exists a serious shortage of range for spring and fall grazing.

The topography of Utah is characterized by a series of parallel mountain ranges and high, narrow plateaus, with interjacent valleys, which extend in a general north and south direction from the north middle to the central part of the state and then sweep in a broad curve to the southwest corner, with the

¹ Utah Agr. Exp. Sta. Bul. 204, p. 11.

Uinta range attached as an east and west spur in the northeastern part of the state. The Raft River range in the northwest corner and the La Sal, Henry and Abajo groups of mountains in the southeast, form important outliers. The remainder of the state consists of low north and south ranges of mountains with broad, flat semi-desert valleys in between, and of deeply dissected semi-desert plateaus.

Precipitation is largely governed by the principal mountain systems. At the higher elevations the annual precipitation is from twenty to thirty inches, sufficient for a fairly dense growth of forest, shrubs, and herbs. The semi-desert and lower plateau areas receive but five to ten inches of rainfall. The narrow strips of lower mountain slopes, inter-montane valleys and adjacent foothills and bench lands receive ten to twenty inches of rainfall and have a growing season that begins during April, conditions favoring spring and fall grazing. At least half of the range land in Utah is semi-desert and suitable only for winter grazing. The higher mountains, estimated to have an area of approximately eleven million acres, seven million of which are in national forest, furnish most of the summer grazing. Only the intermediate lands are well adapted to spring-fall grazing.

The greater percentage of Utah's farm lands, roughly two and one-half million acres, because of the availability of water from the nearby mountain streams or a rainfall sufficient for dry-land agriculture are located on the valley fringes, on bench lands, and in the inter-montane valleys, thus not only reducing the area of spring-fall range, but removing from grazing use the lands formerly of highest forage productivity.

No accurate figures are available on the remaining area of spring-fall range in Utah. Preliminary estimates indicate that there are about nine million acres but this may prove entirely too high when the area is more accurately determined. These foothill range lands for the most part have been utilized longer than any other range type in Utah. The range livestock industry grew to importance early in the economic development of the state. In 1883, thirty-five years after the arrival of the first settlers, there was estimated to be 100,000 cattle and 450,000 sheep in the territory.² During the period 1880-1900, the number of range livestock increased very rapidly. In 1891 there were reported 384,000 cattle and 2,056,000³ sheep, while in 1901 there were 279,000 cattle and 3,537,000⁴ sheep. On January 1, 1931, there were reported to be 344,000 cattle and 2,926,000 sheep in the state.⁵ Thus practically all the range land in the state has been fully stocked for at least forty years. However, the early use was confined largely to the foothill and inter-

² Bancroft, History of Utah, pp. 730-731.

³ U. S. D. A. Yearbook 1891, pp. 312-313.

⁴ Figures obtained from U. S. D. A. Bureau of Agricultural Economics, Salt Lake City, Utah.

⁵ U. S. D. A. Bureau of Agr. Econ., Division of Crop and Livestock Estimates. Utah Annual Livestock Report, Jan. 1, 1931.

montane valleys where there was sufficient forage to provide for the number of stock being grazed. The higher mountain ranges and the semi-desert areas were not used extensively until about 1880. The agencies which have changed the vegetation on the foothill areas therefore, began to exert their influence about eighty years ago.

For convenience in discussion, the spring-fall range covered by this study has been divided into four districts roughly equal in acreage. Major forage types, soil, topography and climate were considered in making this division. The districts are termed: (1) Great Salt Lake, (2) West Central, (3) Upper Sevier Valley, and (4) Uinta Basin. The principal physiographic features in each district determined its name. The Great Salt Lake district includes foothill lands adjacent to the west face of the Wasatch Mountains from the mouth of American Fork Canyon in Utah county north to the Utah-Idaho line in Box Elder County, extending west in Box Elder County to include the foothill ranges north of Great Salt Lake as far as Snowville in Curlew Valley. The West Central district includes the foothill lands along the west face of the Wasatch Mountains from American Fork to Mt. Nebo in Juab County, thence south along the west face of the Pavant and Beaver Mountains to Beaver City in Beaver County. The Upper Sevier Valley district extends south along the west front of the Beaver Mountains from Beaver City to Parowan in Iron County and also includes the foothills and valley fringes of the Sevier River drainage in Garfield, Piute, Sevier and Sanpete Counties. The Uinta Basin district is located in the northeastern corner of the state. It includes the spring-fall range type in the Duchesne River drainage in Duchesne county and a strip paralleling the south and east boundaries of the Ashley National Forest in Uinta County.

The major vegetative types are rather similar on the four districts. Broadly speaking, sagebrush (*Artemisia tridentata*) is the dominant plant species, and grows in association with a varying mixture of grasses, weeds, and a few species of low shrubs. Pinyon-juniper (*Pinus monophylla* and *Juniperus utahensis*) is an important type on all districts except the Great Salt Lake. Oak brush (*Quercus gambelii*) is common on all districts except in the eastern part of the Uinta Basin and the northern part of the Great Salt Lake. Neither of these types, however, is as widespread as the sagebrush association. On burned-over areas of the Great Salt Lake district, downy brome grass (*Bromus tectorum*) has replaced sagebrush as a dominant and often occupies these sites in dense stands associated with alfilaria (*Erodium cicutarium*), little rabbitbrush (*Chrysothamnus* sp.), matchweed (*Gutierrezia sarothrae*), and a few relatively unpalatable species of perennial and annual weeds.

Downy brome is the only important annual grass on the area studied, and is found in quantity only on the Great Salt Lake district. The bunch wheat-grasses (*Agropyron spicatum*, *A. incorne* and *A. tenerum*) and Nevada blue-grass (*Poa nevadensis*) occur on all districts except the Upper Sevier Valley

where short grasses (*Bouteloua gracilis* and *Hilaria jamesii*), replace them to a great extent. Blue stem wheatgrass (*A. smithii*), Sandberg's bluegrass (*Poa sandbergii*), needle and thread grass (*Stipa comata*), rice grass (*Oryzopsis hymenoides*) and bottle brush squirrel tail (*Sitanion hystrix*) occur generally over the area.

Perennial weeds of high palatability are unimportant over the area as a whole. Matchweed, a half shrub, is common in all districts. Black sage (*Artemisia nova*), is an important shrubby plant in sections of the Upper Sevier Valley district.

METHOD OF STUDY

All the areas of range land, which for one reason or another had not been grazed or had been but lightly grazed for many years, that could be found within the district were studied and compared with areas representing ordinary grazed range. Thirty-three areas were found which had been grazed but a little or not at all for from five to over forty years. These preserved areas were chiefly unused portions of cemeteries, upon which the vegetation had been left in its natural condition, or uncultivated tracts adjoining or interspersed with cultivated land upon which grazing had been totally or partially excluded for many years. Nine of these areas showed indications of having been burned over at one time or another. The classification of areas as to length of time protected is as follows:

No. of Years Protected	No. of Areas
5-10	4
11-20	6
21-30	8
31-40	2
Over 40	6
Indefinite as to length of time but sufficient to represent original forage cover	7
Total	33

With the exception of seven, on which no definite historical data could be obtained, the areas have been protected from grazing by livestock for an average of twenty-eight years.

Plots varying from approximately one to two and one-half acres in size, representing typical fenced and unfenced grazed range and including different conditions of slope, soil, and exposure, were selected at random throughout the districts and compared with the ungrazed areas. A total of 101 such plots were studied. These plots were all unquestionably overgrazed. No examinations were made of moderately grazed areas due to their apparent scarcity and to lack of reliable utilization history. In this paper, the term "grazed plots" will designate overgrazed areas.

A careful survey was made of the vegetation on each plot according to the following method. All of the species occurring on each plot were listed. The density of the vegetation—the fraction of the ground surface occupied by

vegetation in terms of hundredths of a complete ground cover—was determined by careful ocular estimate in accordance with the method used by the U. S. Forest Service in making range surveys. The percentage that each species composed of the density of the total vegetation was then carefully estimated. Species which composed less than one per cent of the total density were indicated as being present but were disregarded in the final compilation.

Percentage of palatability⁶ was used in the compilation to express the forage value of the different species. The values used were chiefly those previously determined by careful observations made by Region 4 of the U. S. Forest Service and the Intermountain Forest and Range Experiment Station for use in range surveys and were supplemented by observations during the study. The sum of the products of the density and palatability percentage for each species on a plot, called the "forage factor," was used as a measure for determining the relative grazing value of each area or plot studied. For convenience in further comparisons, the plant species were grouped in the compilation into the following classes: perennial grasses; annual grasses, principally downy brome; good perennial weeds; poor perennial and annual weeds; sagebrush; and shrubs other than sagebrush. Good perennial weeds are perennials with a palatability of 40 per cent or higher; poor perennial weeds are those with a palatability of 35 per cent or less; annual weeds have been grouped with poor perennial weeds. Although in reality it is a half-shrub, matchweed, because of the annual nature of its stem, has been included with poor perennial weeds. Sagebrush is shown separately because of its low palatability value, its predominance over other shrubby plants on the areas studied and because of its special significance in the vegetational changes which have occurred. Other species of *Artemisia* are included with shrubs other than sagebrush, which as a class is relatively higher in palatability.

RESULTS

Great Salt Lake District

The Great Salt Lake Valley was studied in somewhat greater detail than the other three districts, eighteen ungrazed and thirty-nine grazed plots being included. Since much of the range showed evidence of having been burned over at various intervals in the past, opportunity was afforded to compare

⁶ The palatability percentage for a given species is that percentage of the total edible volume of that plant that has been consumed by livestock when the range on which the plant grows is properly utilized. For example: if 60 per cent of the total volume of *Agropyron spicatum* has been eaten at the time when the range is utilized as closely as it should be grazed, this species is said to be 60 per cent palatable. If at the same time only 30 per cent of the total volume of another species in the same association has been utilized, this species would be said to be 30 per cent palatable. The Forest Service has been observing and recording the palatability of range plants under different conditions for the past 20 years and some very reliable records have been built up.

the effect both of fire and of grazing as well as the combined effect of these factors on the original plant cover. The data for these plots are summarized in table I.

TABLE I. *The average density and forage factor of the vegetation under four conditions on the Great Salt Lake district*

Condition	Plots studied for each condition	Average density (hundredths of a complete cover)							Average forage factor
		All vegetation	Perennial grasses	Downy brome grass	Good perennial weeds	Poor perennial and annual weeds	Sagebrush	Shrubs other than sagebrush	
(1)	9	0.39	0.26	0.00*	0.02	0.06	0.04	0.00*	0.242
(2)	9	0.42	0.18	0.09	0.05	0.06	0.01	0.03	0.234
(3)	22	0.38	0.10	0.06	0.03	0.08	0.09	0.02	0.147
(4)	17	0.30	0.04	0.11	0.02	0.11	0.01	0.01	0.108

* Less than 0.005, approximately 0.003.

(1) Unburned and ungrazed.

(2) Burned and ungrazed.

(3) Unburned and grazed.

(4) Burned and grazed.

The Natural Vegetation

The ungrazed plots which showed no evidence of having been burned over for many years are assumed approximately to represent the original natural vegetation of the spring-fall range in this district. The average values for the ungrazed unburned plots indicate that these areas now have a total plant density of approximately 0.4 of a complete cover. Perennial grasses, includ-

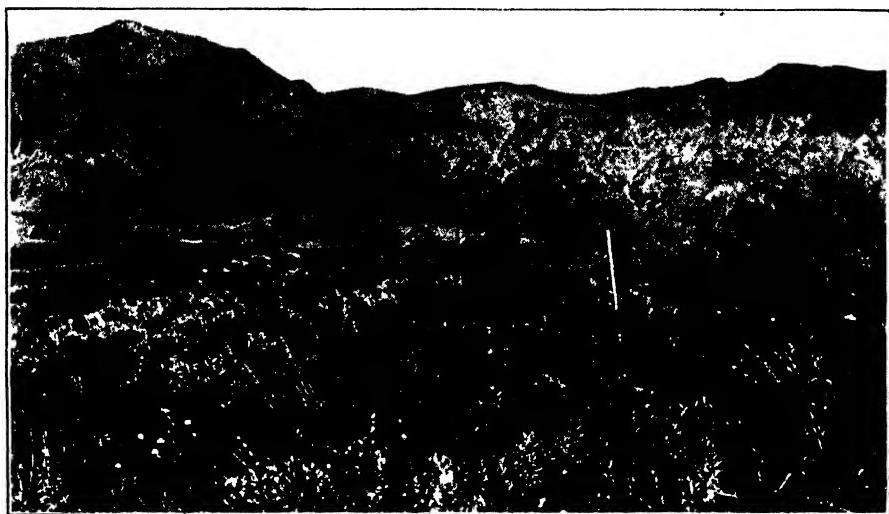


FIG. 1. An area on foothill range near Ogden, Utah, which has been completely protected from grazing and burning for a period of 65 years. Note the predominance of perennial grasses and the low density of sagebrush and weeds.

ing blue bunch wheat (*Agropyron spicatum*), beardless wheat (*A. inerme*), slender wheat (*A. tenerum*), Sandberg's blue (*Poa sandbergii*), and Nevada blue (*P. nevadensis*), with an average density of 0.26, constitute approximately 68 per cent of the total plant cover. All of these grasses are highly valuable for grazing. Downy brome, good perennial weeds and shrubs other than sagebrush are relatively unimportant, occupying in the aggregate a density of 0.03 which constitutes only 7 per cent of the plant cover. Sagebrush, with a density of 0.04 makes up 11 per cent and the remainder or 14 per cent consists of poor perennial weeds. The average forage factor of the ungrazed unburned plots is approximately 0.24.

The Influence of Fire

The protected burned areas when compared with the ungrazed unburned plots indicate the influence fire alone has had on the plant cover of this district. Table I shows that the vegetation on the protected burned plots is slightly higher in average density. However, the density of perennial grasses is 32 per cent less on the protected burned plots, while downy brome is much higher in density and constitutes 22 per cent of the vegetation on the burned plots. There is very little difference in the area occupied by good perennial weeds, shrubs other than sagebrush or poor perennial and annual weeds under the two conditions. Sagebrush has been practically eliminated by fire. The grazing capacity as indicated by the forage factors, however, is slightly lower on the ungrazed burned plots than on the totally protected areas. This is explained by the lower density of highly palatable perennial grasses and a correspondingly higher density of downy brome and other species low in palatability.⁷

The Influence of Grazing

The influence of grazing alone on the original plant cover is indicated by a comparison of the unburned grazed plots with the unburned protected plots. The average density of the vegetation on the unburned grazed plots is only slightly lower than that of the totally protected ones. However, comparison of the two conditions shows striking differences in the composition of the vegetation. The density of perennial grasses on the grazed plots is only 38 per cent as great as on the protected plots. On the other hand, sagebrush is much more prevalent in the plant cover of the grazed plots and dominates the landscape, having a density of 0.09 (24 per cent of the total vegetation), which

⁷ Downy brome, an annual plant that was accidentally introduced into Utah late in the nineteenth or early in the twentieth century makes a quick early growth, beginning in April and ripening about June 1 on the average. It is eaten readily while green but after ripening, the awned character of the seeds and the toughness of the stems make it unpalatable to livestock. Hence, during the month of June and also during the fall grazing period it is of little value as a forage plant on spring-fall ranges. Its palatability is considered to be 40 per cent—only about one-half as much as that of the bunch wheat-grasses.

is about 2.25 times as great as the sagebrush density on the protected plots. Downy brome also has a much higher density on the grazed plots, composing about 15 per cent of the total cover. Poor perennial and annual weeds, principally matchweed, alfilaria, sunflower (*Helianthus* sp.), ragweed (*Ambrosia* sp.), lettuce (*Lactuca scariola integrata*), globe mallow (*Sphaeralcea* sp.), and Russian thistle (*Salsola pestifer*), have a 43 per cent greater density on the grazed as compared to the protected plots, this group representing 21 per cent of the total vegetation of grazed plots. The density of good perennial weeds, principally balsam-root (*Balsamorhiza sagittata*), cut-leaved dock (*B. macrophylla*), mustard (*Sophia* sp.), yarrow (*Achillea lanulosa*), lupine (*Lupinus* sp.), false dandelion (*Agoseris* sp.), and hawk's beard (*Crepis* sp.),



FIG. 2. An area which has been protected from grazing for 15 years but which was severely burned during the first year of protection. Sagebrush is completely destroyed and perennial grasses are lower in density than on adjacent unburned areas. Downy brome and alfilaria are important components in the vegetative composition.

as well as shrubs other than sagebrush, principally bitterbrush (*Purshia tridentata*) and yellow brush (*Chrysothamnus* sp.), is higher on the grazed plots, although these groups occupy but a minor place in the plant cover. The grazing capacity of the unburned grazed range, as indicated by the forage factor, is approximately 40 per cent less than that of the protected areas. Although the density of the plant cover is approximately the same under both conditions, the substitution of sagebrush, downy brome and other plants of inferior forage value for the perennial grasses of high forage value has resulted in a material decline in the grazing capacity of the unburned grazed areas.

The Influence of Burning and Grazing

The influence of grazing and burning combined on the original plant cover is shown by a comparison of the unburned protected and the burned grazed plots. The average density of the vegetation on the burned grazed plots is only 76 per cent as great as that of unburned protected plots. Perennial grasses on the burned grazed plots have only 16 per cent as great a density as on the unburned protected plots and constitute but 14 per cent of the total vegetation. Downy brome is the dominant species and makes up 38 per cent



FIG. 3. A typical heavily grazed but unburned area near the area depicted in Fig. 1 and similar in site. Note the heavy sagebrush density and the scarcity of perennial bunch grasses. Downy brome, alfileria and matchweed make up the greater share of the herbaceous plant cover.

of the total plant density. Poor perennial weeds occupy about twice as much space on the burned grazed plots and represent 37 per cent of all the vegetation. There is but little difference in density of good perennial weeds and of shrubs other than sagebrush and both groups are relatively small in total amount under the two conditions. Sagebrush has been practically destroyed by fire on the burned grazed plots and comprises but 3 per cent of the total vegetation as compared to 10 per cent on the unburned protected plots. The carrying capacity as shown by the forage factor, on the burned grazed plots is only 44 per cent of that on the totally protected plots.

West Central District

Nine protected plots and thirty grazed plots were studied in this district. Range fires have been unimportant and are not considered in this discussion. The data are summarized in table II, series 3 and 4.

The Natural Vegetation

The average values of the protected plots indicate that these areas now have a density of approximately 0.33 of a complete cover and a forage factor of about 0.17. These values are proportionately lower than those of the Great Salt Lake district, and may be explained in part by the fact that soil and



FIG. 4. A heavily grazed area which has been burned over repeatedly. Note the complete absence of sagebrush and perennial grasses. The darker brush-like plants are matchweed. Downy brome and alfilaria constitute the bulk of the vegetation.

moisture conditions are less favorable in the West Central district. In the southern part of the district rocky and dry soils are common and in the north the spring-fall range lands are mostly steep, dry slopes on the lower western front of the Wasatch mountains. There are occasional inter-montane valleys which contain areas of spring-fall range with a high potential grazing capacity but these are in the minority when the whole unit is considered. Perennial grasses, principally blue bunch wheat, beardless bunch, blue stem wheat (*Agropyron smithii*), Sandberg's blue, and rice grass (*Oryzopsis hymenoides*), with a density of 0.19 occupy 56 per cent of the total plant cover. Downy brome and good perennial weeds are relatively unimportant representing only 4 per cent of the plant cover respectively. Poor perennial and annual weeds, principally globe mallow, phlox (*Phlox longifolia*), sunflower, milk vetch (*Astragalus* sp.), and wild lettuce; sagebrush; and shrubs other than sagebrush, principally rabbitbrush (*Chrysothamnus* sp.), gambel oak (*Quercus gambelii*), bitter brush and serviceberry (*Amelanchier alnifolia*), occupy 13, 12, and 11 per cent of the plant cover, respectively.

Influence of Grazing

The protected are compared with the grazed plots to indicate the influence of past grazing practice on the original plant cover of this unit (table II, series 3 and 4). The average density of the grazed plots is 32 per cent lower than the protected plots. Perennial grasses have but 0.02 density which is only 13 per cent of the area occupied by perennial grasses on the protected plots. Sagebrush, with a density of 0.12, occupies 63 per cent of the total cover on grazed plots as compared to a density of 0.01 of this species on protected plots. Downy brome has only a slightly greater density on grazed than on protected plots, possibly because burning is not widespread and also because heavy grazing early in the spring growing season may prevent this annual grass from maturing a normal seed crop.

The density of good perennial weeds as well as shrubs other than sagebrush is lower on the grazed plots. Poor perennial and annual weeds as a class also show a lower density on grazed plots, but the density of matchweed, which is unpalatable to livestock, is decidedly increased.

The decreased total density and the replacement of the highly palatable perennial grasses by sagebrush and other species of low palatability has resulted, as is indicated by the forage factor, in a decrease of 75 per cent in grazing capacity on grazed areas.

Upper Sevier Valley and Uinta Basin Districts

Field work was not carried on in great detail on these districts. The data obtained, however, will serve to indicate the major vegetational changes on grazed range.

Influence of Grazing on Original Cover of Upper Sevier Valley District

The protected are compared with the grazed plots to indicate the major effects of past grazing practice on the original plant cover of this district (table II, series 5 and 6). The data show that the grazed plots have a 37 per cent lower density and a 76 per cent lower forage factor than do the protected plots. The density of good perennial weeds is slightly lower on the grazed plots. Poor perennial weeds and annuals, sagebrush, and shrubs other than sagebrush, have distinctly greater densities on grazed plots, occupying 6 per cent, 47 per cent and 29 per cent of the composition, respectively. Downy brome has no measurable density on the grazed plots of this district. Perennial grasses which are the principal forage resource on the protected plots, occupy only 18 per cent of the composition on the grazed plots.

Influence of Grazing on Original Cover of Uinta Basin District

A comparison of the protected and grazed plots studied on the Uinta Basin district (table II, series 7 and 8), indicates that the average density and the forage factor of grazed plots is 24 per cent and 39 per cent less, respectively, than on protected plots. Perennial grasses have 36 per cent less density on

TABLE II. *The average density and forage factor of the vegetation on protected and grazed plots for all districts*

Series	Plots in series (no.)	Average density (hundredths of a complete cover)					Average forage factor	Condition	District
		All vegetation	Perennial grasses	Downy brome grass	Good perennial weeds	Poor perennial and annual weeds			
1	9	0.39	0.26	0.00*	0.02	0.06	0.04	0.00*	Salt Lake
2	22	0.38	0.10	0.06	0.03	0.08	0.09	0.02	"
3	9	0.33	0.19	0.01	0.02	0.04	0.04	0.03	West Central
4	30	0.23	0.02	0.03	0.01	0.04	0.12	0.01	"
5	3	0.30	0.24	0.02	0.00†	0.01	0.01	0.02	Sevier
6	13	0.19	0.03	0.00	0.00†	0.01	0.09	0.05	"
7	3	0.45	0.22	0.02	0.08	0.05	0.06	0.02	Uinta Basin
8	19	0.34	0.14	0.00	0.02	0.04	0.11	0.03	"

* Less than 0.005—approx. 0.003.

† Less than 0.005—approx. 0.002.

‡ Less than 0.005—approx. 0.001.

grazed than on protected plots but still represent 42 per cent of the plant cover. Downy brome has no measurable density on grazed plots. The density of good perennial weeds is only 25 per cent as great on grazed as on protected plots. Sagebrush, on the other hand, has an 81 per cent higher density on grazed plots where it occupies 32 per cent of the plant cover. Shrubs other than sagebrush likewise have a higher density on grazed plots but occupy only 9 per cent of the plant cover.

SUMMARY AND CONCLUSIONS

Spring-fall range in Utah, which includes the lower mountain slopes and the adjacent foothills and valley fringes, has been heavily grazed for more than forty years.

Observations show that areas of spring-fall range, long protected from grazing and fire, such as cemeteries and field corners, support a good cover of plants palatable to livestock. The chief forage plants on these areas in every case in four districts studied, include highly palatable perennial grasses, chiefly blue bunch wheatgrass (*Agropyron spicatum*), beardless wheat (*A. inerme*), blue stem wheat (*A. smithii*), Sandberg's blue grass (*Poa sandbergii*), and Nevada bluegrass (*P. nevadensis*). Perennial grasses represent 49 to 81 per cent of the total plant cover. Sagebrush (*Artemesia tridentata*) is unimportant on such areas, occupying an average of slightly less than 10 per cent of the plant cover. Annual grasses, principally downy brome (*Bromus tectorum*), weeds, and shrubs other than sagebrush are all relatively unimportant.

Observations on promiscuously burned areas which have long been protected from grazing indicate that burning tends to deplete the stand of perennial grasses and to allow annual grasses, chiefly downy brome, to increase sharply in density. The sagebrush cover is largely destroyed by burning. The total plant density of burned protected plots is about the same as on those totally protected. There is, however, a slight decrease in the grazing capacity of burned protected plots.

Observations on areas which have been subjected both to promiscuous burning and to heavy grazing show that a combination of these factors has seriously reduced the total density of the plant cover, and has depleted the stand of perennial grasses nearly 85 per cent. The sagebrush cover likewise has been reduced 80 per cent. Annual grasses and poor perennial and annual weeds are predominant. These changes in the plant cover due to fire and grazing have caused a reduction of over 50 per cent in the grazing capacity of the spring-fall range.

Observations on areas subjected to heavy grazing only, show in every case a serious depletion of perennial grasses, a decided increase in density of sagebrush, in some instances a sharp increase in the density of poor perennial weeds and annual grasses and a decrease in the total plant density. These vegetational changes have resulted in reductions of 40 to 75 per cent in the grazing capacity of the areas studied in four districts.

STUDIES IN POPULATION PHYSIOLOGY: THE RELATION OF
NUMBERS TO INITIAL POPULATION GROWTH IN
THE FLOUR BEETLE *TRIBOLIUM CONFUSUM*
DUVAL¹

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Chapman ('28), working with the confused flour beetle *Tribolium confusum* Duval, presented evidence demonstrating that a condition of equilibrium, measured in terms of number of individuals per gram of flour, is eventually reached within each population which is approximately uniform irrespective of the environmental size or the initial population density. In table III of his paper, reproduced herewith, he has recorded data, which in addition to supporting his own conclusions, open to experimentation another phase of the problem. Allee ('31), interested in reviewing the effects of crowding on organisms, has analyzed this data. He shows that for the first periods in the development of the beetle population, namely eleven and twenty-five days, the greatest increase in numbers, in terms of eggs and early instar larvae per female day, comes at the initial population of four, while initial populations of eight or sixteen show a more rapid increase at eleven days than that given when only one pair was present. About this phenomenon, Allee remarks ('31, p. 180), "This indicates that there is an optimum initial population-medium relationship, which, for certain volumes of medium, is different from that given by the smallest population present." Chapman's original data are presented in table I together with a recalculation to show the rate of increase per female day at all population densities tried.

The work to be reported in this paper has been directed towards finding by more extensive experiments whether the initial rate of population growth is usually greater in these beetle populations when more than one pair of beetles is present.

CONDITIONS OF EXPERIMENT

The biology of *Tribolium confusum* has been adequately studied by Chapman ('18 and '24), Dean ('13), and Brindley ('30), hence it is only necessary at this point to observe that all stages of its life-cycle are passed in pulverized grains. In all of the experiments conducted here, the medium used was either patent white flour, or finely sieved whole wheat flour; these permit an accurate count of the eggs and larvae. The technique of examination of the flour

¹ The author wishes to indicate his indebtedness to Professor W. C. Allee, of the University of Chicago, for suggestion of the problem, and co-operative counsel.

TABLE I
A. Original data from Chapman Table III

Days	Grams of flour					
	32	32	32	32	32	32
0	.062	.125	.25	.5	1.0	2.0
11	1.15	5.500	9.00	16.0	27.0	42.0
25	2.50	12.000	19.00	20.0	30.0	38.0
54	11.00	27.000	32.00	30.0	43.0	55.0
69	28.00	31.000	30.0	29.0	46.0	47.0
81	30.00	44.000	42.00	43.0	53.0	53.0
104	40.00	43.000	38.00	42.0	52.0	44.0
123	45.00	43.000	39.00	50.0	50.0	46.0
139	42.00	47.000	42.00	44.0	50.0	45.0

B. Recalculated in terms of rate of increase of population per adult female day

Days	Grams of flour					
	32	32	32	32	32	32
0	0.0	0.0	0.0	0.0	0.0	0.0
11	3.3	8.0	6.5	5.8	4.9	3.8
25	3.2	7.6	6.0	3.2	2.4	1.9
54	6.5	8.0	4.7	2.2	1.5	1.0
69	12.9	7.1	3.4	1.6	1.3	.66
81	11.8	8.6	4.1	2.1	1.3	.64
104	12.3	6.6	2.9	1.6	1.0	.42
123	11.7	5.5	2.5	1.6	.81	.37
139	9.6	5.4	2.4	1.2	.71	.31

for immature stages was adopted from Chapman ('18), and simply consisted of passing beetle-populated flour through standard meshes of silk bolting cloth as a means of isolating all individuals. The experiments were run at a constant temperature of 28° C. under stable humidity.

To duplicate Chapman's set-up, as used in connection with securing the data shown in his table III, 32 grams of flour were placed into a series of similar glass bottles which had been autoclaved just previous to the start of the experiment. The depth of the flour in each bottle so prepared was approximately two centimeters, resulting in volumes which were equal both in weight and in surface exposure. An experiment usually consisted of four such preparations with one pair of *Tribolium* in the first bottle, two pairs in the second bottle, four pairs in the third bottle, and eight pairs in the last bottle, thus providing for a geometric increase of beetles within a constant-sized environment. Populations of thirty-two and sixty-four beetles were tried at the start, but were discontinued as soon as it was discovered that they uniformly present a relatively low rate of reproduction per female day. All individuals used were chosen at random from the closely inbred stock cultures. The set-up was then incubated 11 days, and readings on population size were made, whereupon, in those experiments run to twenty-five days, the flour was

TABLE II. *Number of eggs produced after 11 days of incubation*

Exp. no.	Adults at start				Adults at start			
	2	4	8	16	2	4	8	16
	Number of eggs				Rate per female day			
I	35	100	120	116	3.18	4.54	2.72	1.27
II	40	130	150	100	3.63	5.81	3.27	1.09
III	60	110	122	150	5.45	5.00	2.72	1.63
VIII	44	76	116	120	4.00	3.45	2.54	1.27
IX	16	100	134	124	1.45	4.54	3.00	1.40
X	34	76	38	100	3.09	3.45	.85	1.09
XI	20	80	166	136	1.81	3.63	3.63	1.45
XII	4	130	130	140	.36	5.81	3.09	1.60
XIII	20	114	170	160	1.81	5.09	3.81	1.67
XIV	38	66	150	160	3.45	3.00	3.27	1.67
XVIII	0	60	0	100	0.00	2.72	0.00	1.09
Means	28	94	117	127	2.56	4.27	2.59	1.38

TABLE III. *Number of larvae produced after 11 days of incubation*

Exp. no.	Adults at start				Adults at start			
	2	4	8	16	2	4	8	16
	Number of larvae				Rate per female day			
I	28	56	92	30	2.54	2.54	1.00	0.34
II	30	46	88	144	2.72	2.09	2.00	1.63
VII	26	32	42	80	2.36	1.45	.94	.90
VIII	20	30	42	50	1.81	1.36	.94	.56
IX	12	42	48	48	1.09	1.90	1.09	.54
X	4	36	4	34	.36	1.45	.09	.38
XI	3	42	40	44	.27	1.90	.90	.50
XII	4	38	48	42	.36	1.72	1.09	.47
XIII	4	54	90	80	.36	2.40	1.81	.90
XIV	8	32	48	32	.72	1.45	1.09	.36
XVIII	5	28	32	120	.45	1.27	.72	1.36
III	4	30	38	48	.36	1.36	.85	.54
IV	3	32	40	46	.27	1.45	.90	.50
VI	16	32	70	110	1.45	1.45	1.58	1.23
XVI	1	44	70	74	.09	2.00	1.58	.83
XVII	2	30	47	118	.18	1.36	1.05	1.34
XV	5	32	50	110	.45	1.45	1.12	1.23
Means	10	37	57	71	.93	1.68	1.10	.80

changed to eliminate excrement, and the eleven day eggs, larvae, and adults were returned to their respective bottles for fourteen more days of incubation.

EXPERIMENTATION

The data accumulated is presented in the tables: first, that dealing with 11 day counts of eggs as listed in table II; second, 11 day counts of larvae

as in table III; third, rates per female day for eleven days as combined from tables II and III, found in table IV; fourth, table VI listing the number of eggs for twenty-five days; fifth, table VIII listing the number of larvae for twenty-five days, and sixth, a combination of the 25 day number of eggs and larvae, expressed in table VIII in terms of combined rate per female day. Also, tables showing statistical analysis, and graphic comparisons are presented.

TABLE IV. *Combined rates per female day for both eggs and larvae after 11 days of incubation*

Exp. no.	Adults at start			
	2	4	8	16
	Rate per female day			
I	5.72	6.08	3.72	1.61
II	6.35	7.90	5.27	2.72
III	5.81	6.36	3.57	2.17
VIII	5.81	4.81	3.48	1.83
IX	2.54	6.44	4.09	1.94
X	3.45	4.90	.63	1.47
XI	2.08	5.53	4.53	1.95
XII	.72	7.53	4.18	2.07
XIII	2.17	7.54	5.62	2.57
XIV	4.17	4.45	4.35	2.03
XVIII	.45	3.99	.72	2.45
Means.....	3.57	5.95	3.65	2.07

Tables II, III, and IV record counts of eggs, larvae and mean rates resulting from eleven days of incubation of similar-sized environments containing two, four, eight, and sixteen adult beetles with equal number of males and females in each bottle. The interest, in these experiments, is to determine whether any especial population produces more eggs and early instar larvae in eleven days time than the others, and, if so, does this hold well enough to be significant?

Table II, recording the number of eggs only, shows that out of eleven experiments there are three in which the initial population of two is producing more eggs at eleven days than the other sized groups. There are seven cases where the initial population of four presents the peak, and one case in which the eggs from initial populations of the four and the eight are equally high. In terms of averages the initial group of four is producing approximately one and a half times as many eggs as are those of two or eight. The latter are very similar, with the eight showing a slight indication of peak over the two. The initial populations of sixteen clearly show the fewest eggs.

Table III lists the number of larvae produced after eleven days of incubation and presents essentially the same situation as table II. Out of a total

seventeen cases there are three instances of peak at the smallest initial population, twelve where the initial group of four is highest, one case in which the peak falls at eight, and one where the seeded population of sixteen leads. There are also two experiments in which the initial populations of two and four are equal. Returning to a consideration of averages, the same relationship as that displayed in table II is apparent. The initial population of four has produced most larvae, that of eight is slightly higher than that of two, while the largest initial population has yielded the fewest larvae. It might be pointed out from table III that the number of larvae produced in the initial population of two seem to be present in either one or two groups according to numbers. There is that class where the larvae average about four, and the other where the mean number produced at eleven days seems to be about twenty-two. This tends to indicate a certain correlation between specific experiments, but the explanation is not apparent at this time.

Table IV, expressing the combined rates per female day after eleven days of incubation for both eggs and larvae, clearly substantiates the general trend of initial population growth as displayed by tables II and III. In these combined figures, there is one case where the peak falls at the initial minimum population, and ten instances at the population of four. Similarly, in terms of the mean, the latter is decidedly above the others; that of eight is slightly in excess of the minimum while, as always, the maximum initial population tried has reproduced at the slowest rate.

TABLE V. *Showing the statistical significance of the rates of reproduction of Tribolium after 11 days of incubation*

A. Rate of egg production per female day

Original population	Mean rates	Probability
2 cf. with 4.....	2.56 cf. with 4.27	.0140
4 cf. with 8.....	4.27 cf. with 2.59	.0008
8 cf. with 16.....	2.59 cf. with 1.38	.0040

B. Rate of larvae production per female day

Original population	Mean rates	Probability
2 cf. with 4.....	.93 cf. with 1.68	.0028
4 cf. with 8.....	1.68 cf. with 1.10	.0004
8 cf. with 16.....	1.10 cf. with .80	.0064

C. Total rate of reproduction per female day

Original population	Mean rates	Probability
2 cf. with 4.....	3.57 cf. with 5.95	.0080
4 cf. with 8.....	5.95 cf. with 3.65	.0006
8 cf. with 16.....	3.65 cf. with 2.07	.0040

Table V, a statistical analysis of the results listed in tables II, III, and IV, has been calculated according to the method of Student ('25) for testing significances of small numbers. The results, stated in terms of the probability, show these experiments to be statistically significant. The probability in this analysis represents the chance of getting, in a random sample, a deviation as great as the one observed. It is evident that the numbers

listed in the tables fluctuate considerably within a single initial population size. This is to be expected, however, on the basis of individual variability between the adults introduced at the start of the experiment, on the basis of certain ecological forces at work within each population, and on the basis of accidents to the beetles entertained during the course of the experiment.

The data of tables VI, VII, and VIII, recording the number of larvae

TABLE VI. *Number of eggs produced after 25 days of incubation*

Exp. no.	Adults at start				Adults at start			
	2	4	8	16	2	4	8	16
	Number of eggs				Rate per female day			
I	6	40	60	70	.24	.80	.60	.34
XI	40	36	90	86	1.60	.72	.90	.42
XII	44	100	80	90	1.76	2.00	.80	.44
XIII	38	30	40	42	1.52	.60	.40	.20
XIV	60	66	50	46	2.40	1.32	.50	.22
XVI	20	26	35	21	.80	.52	.34	.10
XVII	36	50	54	50	1.44	1.00	.56	.24
XVIII	34	36	18	15	1.36	.72	.17	.07
Means	34	48	53	52	1.39	.96	.53	.22

TABLE VII. *Number of larvae produced after 25 days of incubation*

Exp. no.	Adults at start				Adults at start			
	2	4	8	16	2	4	8	16
	Number of larvae				Rate per female day			
I	100	142	170	168	4.00	2.84	1.69	.84
II	100	130	200	164	4.00	2.60	2.00	.81
III	27	130	162	100	1.08	2.60	1.61	.49
IV	16	88	64	110	.64	1.76	.64	.54
V	1	45	xxx	104	.04	.89	0.00	.52
VI	92	76	230	220	3.68	1.52	2.29	1.09
XI	10	70	90	110	.40	1.40	.89	.54
XII	10	130	124	82	.40	2.60	1.24	.40
XIII	26	110	132	170	1.04	2.20	1.32	.84
XIV	18	44	108	58	.72	.88	1.04	.28
XV	32	88	110	154	1.28	1.76	1.09	.76
XVI	10	88	120	142	.40	1.76	1.20	.70
XVII	28	62	100	234	1.12	1.24	1.00	1.16
XVIII	30	94	102	210	1.20	1.88	1.01	1.04
Means	35	92	122	144	1.42	1.85	1.30	.71

and eggs produced by the beetles after twenty-five days of incubation, begin to show a change of trend in terms of reproductive peak. Arbitrarily, the term "initial reproductive rate" begins to break down at the 25 day reading,

TABLE VIII. *Combined rates per female day for both eggs and larvae after 25 days of incubation*

Exp. no.	Adults at start			
	2	4	8	16
	Rate per female day			
I	4.24	3.64	2.29	1.18
XI	2.00	2.12	1.79	.96
XII	2.16	4.60	2.04	.84
XIII	2.56	2.80	1.72	1.04
XIV	3.12	2.04	1.54	.50
XVI	1.20	2.28	1.54	.80
XVII	2.56	2.24	1.56	1.40
XVIII	2.56	2.60	1.18	1.11
Means.....	2.55	2.79	1.90	.97

and the type of population size constancy discussed by Chapman ('28) begins to occur among the larger groups of beetles. From the data of table VIII it can be seen that the rates per female day have dropped in comparison to those displayed for eleven days in table IV. There still remains a slight peak at the initial population of four in terms of the total averages, and in terms of the number of larvae. Where eggs are concerned, however, the peak has shifted to the initial population of two (table VI). After twenty-five days the female rate has decreased the maximum amount in the initial groups of four, eight, and sixteen, and the least in the two. This indicates that there has been a shifting of relationships within the populations. The fact that the larvae are slightly more abundant in the seeded population of four at twenty-five days than in the initial minimum population suggests there has been a carrying over of the 11 day peak.

Table IX, analyzed in the same way as table V, demonstrates no signifi-

TABLE IX. *Showing the statistical significance of the rates of reproduction of *Tribolium* after 25 days of incubation**A. Rate of egg production per female day*

Original population	Mean rates	Probability
2 cf. with 4.....	1.39 cf. with .96	.5660
4 cf. with 8.....	.96 cf. with .53	.3944
8 cf. with 16.....	.53 cf. with .22	.3466

B. Rate of larvae production per female day

Original population	Mean rates	Probability
2 cf. with 4.....	1.42 cf. with 1.85	.2400
4 cf. with 8.....	1.85 cf. with 1.30	.4962
8 cf. with 16.....	1.30 cf. with .71	.1320

C. Total rate of reproduction per female day

Original population	Mean rates	Probability
2 cf. with 4.....	2.55 cf. with 2.79	.5652
4 cf. with 8.....	2.79 cf. with 1.90	.0026
8 cf. with 16.....	1.90 cf. with .97	.1720

cance between the populations at twenty-five days except the mean difference existing between the initial populations of four and eight. This is to be expected since the populations are departing from their earlier growth relationships, but have not, at twenty-five days, reached their equilibrium point.

Figure 1 plots the rate of production of eggs and larvae at eleven days as

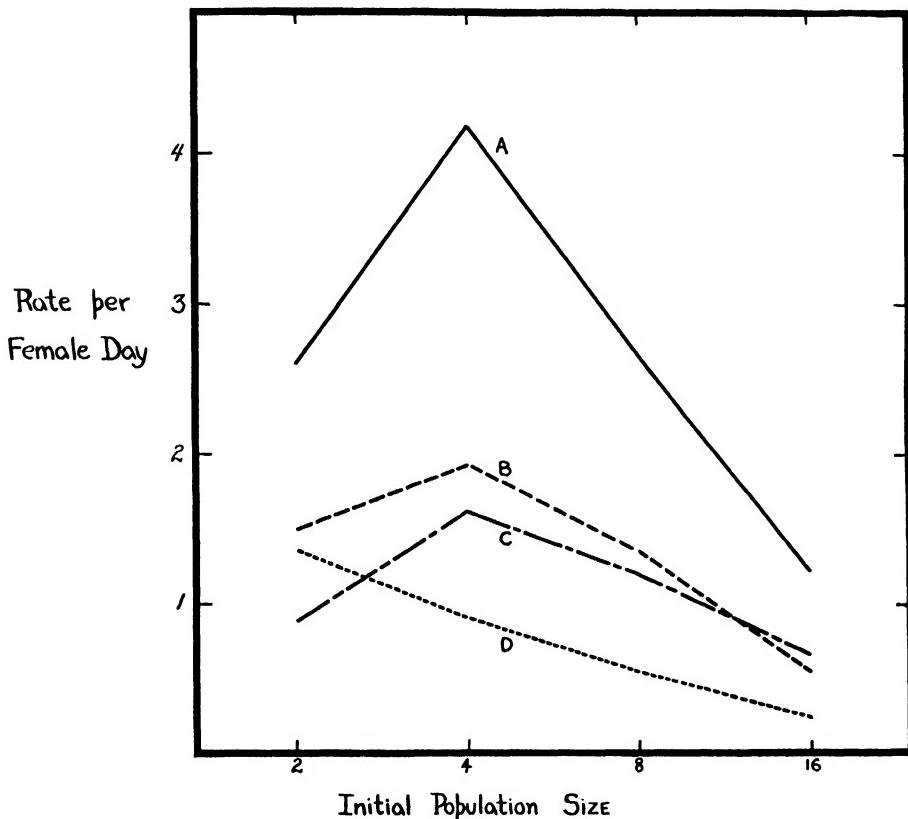


FIG. 1. Graph comparing average rate of egg and larvae production for 11 and 25 days.

A = Eggs (11 Days)

B = Larvae (25 Days)

C = Larvae (11 Days)

D = Eggs (25 Days)

contrasted with twenty-five days. The high peak is seen to occur at the initial population of four for eggs and larvae at eleven days. The 25 day representations, not being statistically significant, are not particularly valuable.

The second graph compares the data of Chapman with that presented in this paper. It can be seen that the general trend of the two 11 day data is essentially similar with a decided peak falling at the initial population of four. Chapman's figures run consistently higher in both cases, and analysis of these variations calls for direct experimentation.

CONCLUSIONS

The foregoing data show that an optimum population-medium relationship exists in early stages of cultures of *Tribolium confusum*, in which two pairs of adult beetles in 32 grams of flour typically produce more eggs per day than in the other set-ups. Later the rate decreases in the larger population den-

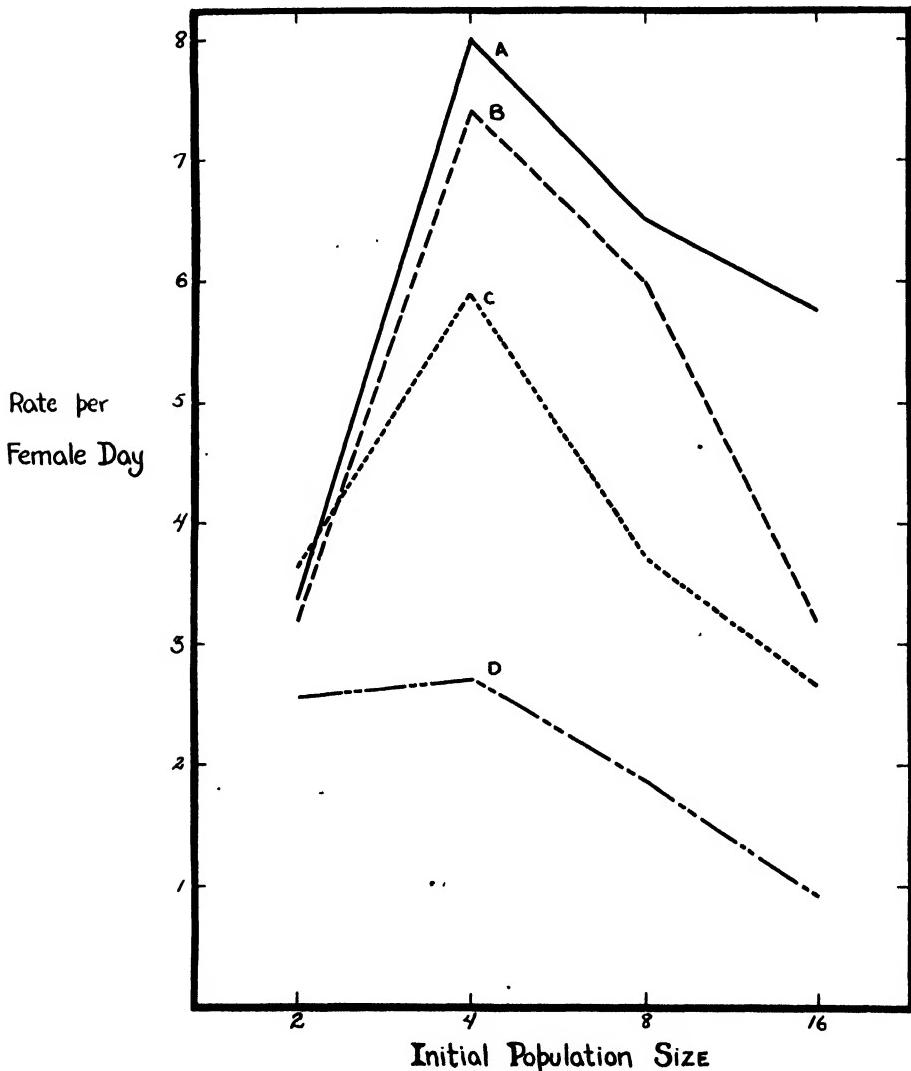


FIG. 2. Comparison of Chapman's data with that presented in present paper.

- A = Chapman (11 Days)
- B = Chapman (25 Days)
- C = Park (11 Days)
- D = Park (25 Days)

sities until the populations come to equilibrium as described by Chapman ('28). It is interesting to note that these beetles show a different type of relationship than do *Drosophila* (Pearl and Parker, '22) which have their highest rate of reproduction per female day with an initial population of only one pair of flies. In this respect these results resemble the observations of Robertson ('24) and Peterson ('29), who find that under appropriate conditions two infusoria will reproduce more rapidly in the same vessel than if they are isolated in the same volume of culture medium. The theoretical implications of this general type of crowding phenomenon have recently been considered by Allee ('31) as a phase of animal aggregations or physiology of the mass and need not be emphasized here.

No attempt has been made in this paper to discuss the dynamic factors operative among these beetle populations; particularly those forces resulting in the type of initial population peak indicated here. This analysis is now underway and its report is reserved for future publication.

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TRANSPIRATORY ORGANS OF *LARREA TRIDENTATA* AND THEIR ECOLOGICAL SIGNIFICANCE

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Plants of the southwestern desert are commonly divided into two groups—perennials with various devices for conserving and economizing the water supply, and annuals which are in no particular way adapted to endure shortage of water. The former class of plants is further subdivided into succulents, plants whose internal environment is not xeric at all, and other plants which do not store water, but which are believed to economize greatly the water at their disposal. These latter plants are often described as having reduced transpiratory surface, sunken stomata, waxy or hairy leaves, and high osmotic pressure. *Larrea tridentata* (*Covillea tridentata*, creosote bush), which colonises the driest areas around Tucson, is considered to belong to this group.

Recent work of Maximov ('17, '29), Stocker ('23), Alexandrov ('24) and others, has shown that various "xerophytes" and hog plants do not, in fact, transpire any less than so called "mesophytes," nor is their leaf area necessarily reduced in comparison with mesophytes. The following notes embody sundry observations of this nature on the morphology of *Larrea*.

Larrea tridentata is a perennial, with small sticky resinous leaves, arranged oppositely along a frequently branched stem. The leaves are equal-pinnate, and in dry weather are sometimes stuck together along their adaxial faces. The inclination of the leaves to one another seems to depend upon the amount of rain, or the water content of the soil.

If *Larrea* exhibits morphological adaptations to its dry environment, these adaptations will best be brought out by comparing the plant with a mesic plant growing in the same climate, but in moister soil conditions. A privet hedge (*Ligustrum* sp.) in Tucson was chosen for this purpose. The following comparisons were made:

- (1) Ratio of leaf surface to total surface of aerial organs.
- (2) Frequency and distribution of stomata.
- (3) Anatomy of stomata.
- (4) Rate of drying out of cut twigs.
- (5) Water content of leaves.
- (6) Suction pressure of roots.
- (7) Conductivity of stems for water.

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(1)

A small bush of *Larrea* was dug up, and all the leaves picked off. Two thousand leaves were counted and weighed, and the rest weighed, to obtain an estimate of the total number of leaves. The area of a representative sample of leaves was found by tracing the outlines on paper, and measuring the areas with a planimeter. Finally the total area of the branching system was estimated by cutting the branches up into pieces of uniform diameter, and measuring the lengths and diameters of the pieces. Exactly the same procedure was then carried out upon a small privet bush.

(2)

The number and size of the stomata on the leaf could not be found by Lloyd's method of tearing off the epidermis ('08). If the leaf is put into a solution of celloidion in ether, however, and the film of celloidion pulled off when hardened, a clear imprint of the epidermis and stomata is obtained, which can be examined under the microscope, and from which measurements can be taken of stomatal frequency. Stomata occur on both sides of the leaf of *Larrea*, in the proportion of ten on the adaxial face to fifteen on the abaxial face. No significant difference between stomatal frequency at the top and bottom of the bush was found. The same procedure was repeated on the privet bush. The result of the comparisons is given in table I.

TABLE I. Comparison of *Larrea* and *Ligustrum* bushes

	<i>Larrea</i>	<i>Ligustrum</i>
Total area of aerial parts.....	4426 cm. ²	1769 cm. ²
Total leaf area (both sides).....	4906 "	1516 "
Ratio of leaf area to total area.....	0.91	0.86
Number stomata per cm. ² adaxial.....	24,000	none
abaxial.....	36,000	83,000
Total number of stomata.....	120,000,000	63,166,000
Approx. ratio: stom. to total area.....	27,500	36,000

Since the stomata of both *Larrea* and *Ligustrum* are functional, comparative estimates of the pore sizes would have very little significance. An inspection of figure 1, however, indicates that the stomatal aperture in *Larrea* is bigger than that in *Ligustrum*.

Far from having a reduced leaf surface *Larrea* has a greater leaf surface for the total area of the plant than *Ligustrum*. The epidermal cells of *Ligustrum* are, however, smaller, so that the number of stomata in *Ligustrum* is somewhat greater than the number in *Larrea*, referred to total area as a standard.

The xeric character of *Larrea* does not lie in a reduced leaf surface. Nor could the difference in stomatal frequency account for the vast difference in water requirements of the two plants. Estimates of the probable errors of the above figures were not made, since the aim of the experiment is to compare two individual bushes, but experience would not lead one to expect errors greater than 10 to 15 per cent.

(3)

The third comparative test made concerned the anatomy of the stomata. Surface sections and transverse sections of leaves of *Larrea* and *Ligustrum* were cut, stained and mounted. Sketches of typical stomata are shown in figs. 1 and 2. It is surprising that the stomata of *Larrea* do not show any of the anatomical modifications believed to reduce evaporation. The highly

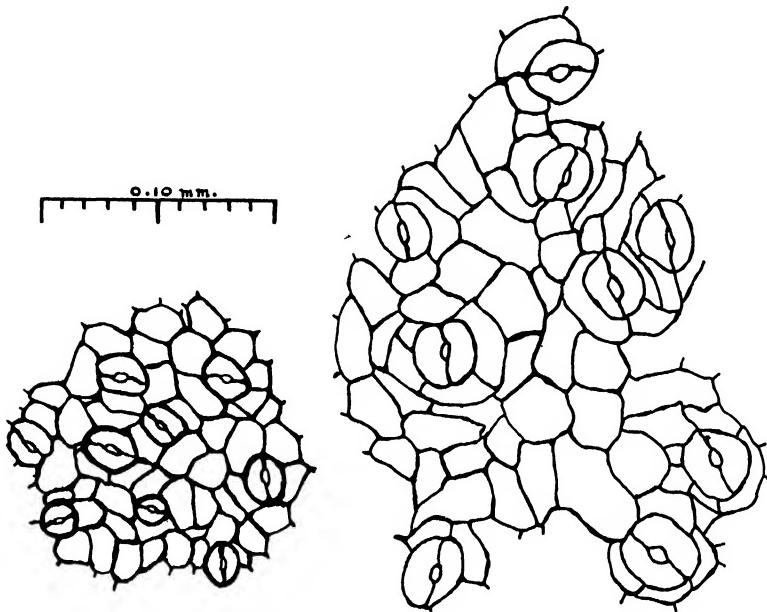


FIG. 1. Portions of the lower epidermis of *Larrea* (right) and *Ligustrum* (left), to the same scale, showing size of cells and number of stomata.

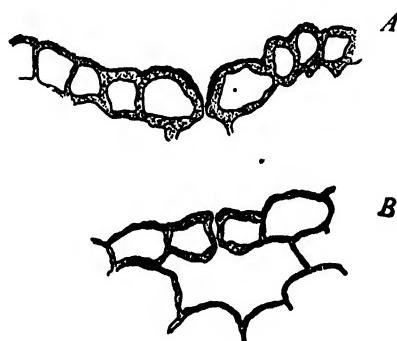


FIG. 2. Transverse sections of stomata of *Larrea* (A) and of *Ligustrum* (B), to the same scale.

cuticularised sunken stomata found in *Ephedra* and *Dasylyrion* have no parallel in *Larrea*. The resin on adult leaves does not apparently block the stomata under ordinary conditions, for prints of the open pore were always obtained when the leaves were dipped in celloidion. The hairs are not thickly scattered, but the cuticle is thicker in *Larrea* than in *Ligustrum*. Cuticular transpiration has not, however, been shown to play an important part in ordinary plants.

(4)

To gain some idea of the rate of water loss through known numbers of stomata, and under conditions of drought, cut twigs of the two plants were allowed to dry out, and were weighed at intervals. Twigs of *Larrea* and *Ligustrum* were picked early in the morning. Their ends were sealed with celloidion, and they were immediately weighed. They were then laid in the

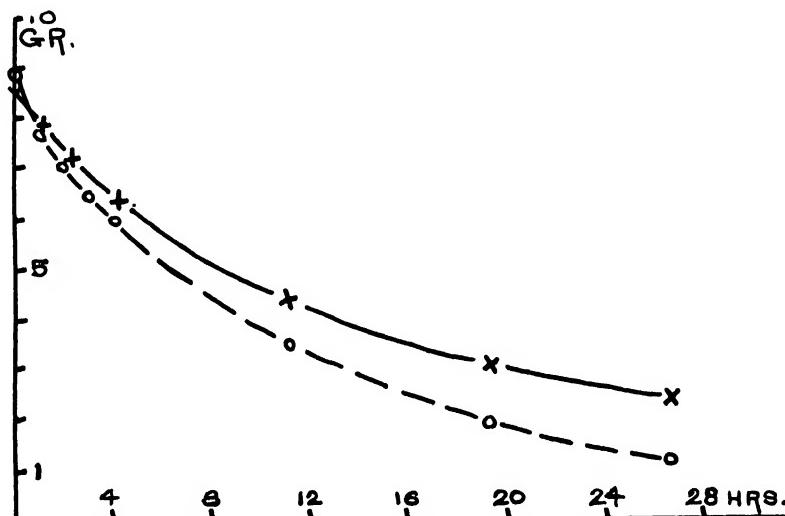


FIG. 3. Curves showing the loss of weight of twigs of *Larrea* (solid line) and of *Ligustrum* (broken line) as they dry out. All points except those at 19 hours are the means of five twigs.

sun in a greenhouse, and weighed at intervals for the next 27 hours. The results are shown in fig. 3.

Judged on a basis of initial weight, *Ligustrum* loses more water in the time of the experiment than *Larrea*. The difference is 1.61, for which $t = 8.46$, $n = 8$, and P is less than 0.01—a difference clearly significant.² This does not take into account the fact that the leaf areas per unit weight of the two genera differ. The leaves from all the twigs were picked off, counted, and dried in an oven. The areas of representative samples were also found. These results are summarized in table II.

² Fisher, R. A. 1928. Statistical methods for research workers. London.

TABLE II. *Particulars of leaf structure, etc., of samples 1 to 3 of Larrea and Ligustrum*

	<i>Ligustrum</i>			<i>Larrea</i>		
	1	2	3	1	2	3
Mean leaf area	2.36 cm. ²			0.36 cm. ²		
Total leaf area	172	306	188	499	272	281 cm. ²
Stomatal frequency						
adaxial	none			24,000		
abaxial	83,000			36,000		
Total no. stomata	15.7	25.5	14.3 mill.	15.0	8.16	8.45 mill.
Net water loss, grms. (27 hours)	4.069	6.895	3.425	6.238	3.480	3.362
Water loss per no. stomata..	269	270	241×10^{-8}	420	426	400×10^{-8}
Water cont. % dry weight ..	68	69	69	62	57	58

(5)

The mean value of the ratio: water loss to total number of stomata in *Larrea* is 1.6 times the value in *Ligustrum*, an increase of 60 per cent. That this difference is significant is clear from a statistical analysis of the difference, using Fisher's "t" table. The difference is 155, $t = 12.4$, $n = 4$, and P is less than 0.01. The xeric characters *Larrea* might be expected to have are reduced leaf area and modified stomata; but its rate of water loss, under conditions of drought, and referred to these two characters, shows that *Larrea* is much less economical than *Ligustrum*, and, as far as inferences can be drawn from the water loss of cut twigs, a creosote bush is capable of losing as much water in a day as a privet bush of comparable size, provided the stomata remain open.

This last reservation can be removed, for, on a warm sunny day, when there had been no rain for about two weeks, the stomata of *Larrea* were not observed to close until 4 P.M. Any regulation to cut down the transpiration must in this case have been physiological, governed by some factor such as the osmotic pressure of the leaves.

(6)

To compare the suction pressures of *Larrea* and *Ligustrum*, roots of the two plants were cut up into slices and weighed, after which they were put into sugar solutions of different concentrations, ranging from 0.1 to 1.5 normal. After 45 minutes in these solutions, the slices were taken out, carefully dried and weighed again. The sugar solution in which the weight changed least was assumed to have an osmotic pressure most nearly the suction pressure of the root. Great value cannot be ascribed to such experiments, for the suction pressure depends markedly upon the past history of the individual plant used. It was interesting, however, that the suction pressure of *Ligustrum* by this method was around 7 atmospheres, while that of *Larrea* was greater than 25 atmospheres.

(7)

In 1918 Farmer ('18) found interesting differences between the conductivity for water of shoots of evergreen and deciduous plants. A simple form of his apparatus was set up, and the conductivities of *Larrea* and *Ligustrum* shoots compared. The rate of flow through the stem was assumed to be proportional to the area of the stem and to the pressure behind the flow, and inversely proportional to the length of the stem, so that:

$$R = \frac{KPA}{L},$$

where R = rate of flow, P = pressure, L = Length, and A = area of stem. K is a constant (the specific conductivity.) On these assumptions, the ratio of conductivities of the two stems K_1/K_2 is given by:

$$\frac{K_1}{K_2} = \frac{R_1}{R_2} \times \frac{A_2 L_1}{A_1 L_2}.$$

The pressure cancels out, for the same pressure from the tap was forced through samples of the two stems at once. For the details of experimentation the reader is referred to Farmer's paper.

The results are interesting. A constant head of water was forced through stems of the two plants under investigation. The rate at which water passed through the two twigs was measured with a stop watch. The lengths of the stems were then measured, and the area of wood obtained by drawing the wood in outline under the low power of the microscope, and measuring the areas with a planimeter. The values for K_1/K_2 are given in table III.

TABLE III. *Ratio of conductivity of Larrea to conductivity of Ligustrum*

Young <i>Larrea</i>	0.915	0.822	0.845
Older <i>Larrea</i>	0.622	0.610	0.757

An older twig of *Larrea*, then, has little more than half the specific conductivity for water of a privet stem. The young stems more nearly approach the same specific conductivity.

The evidence seems to add further support to Maximov's suggestions, namely, that the secret of drought resistance is not to be sought in anatomical or morphological characters, but in the property of the protoplasm to withstand desiccation. In the hot dry season *Larrea* becomes quite inactive. Whereas *Ligustrum* under these conditions would wilt and not recover, *Larrea* can recover at the first adequate shower of rain. It is on its power to recover from wilting, rather than resistance to wilting, that its success as a desert plant depends. The outward sign of this may be the high osmotic pressure and suction pressure of the cells of *Larrea*.

The observations reported are too scanty to warrant any further discussion, but suggest possible lines of investigation.

SUMMARY

Larrea does not store water to any marked extent for the water content of leaves and stems is less than that of a typical mesic evergreen, the privet. It must be borne in mind, however, that the privet was irrigated, while the *Larrea* was not.

The relative leaf surface of *Larrea* is not reduced, nor has a *Larrea* bush fewer stomata than a privet of the same size.³

The stomata of *Larrea* show no anatomical adaptations to conditions of water shortage, and are functional and open in the daytime in March.

The water loss from drying shoots of *Larrea* is actually greater than the loss from privet, calculated on the basis of loss per number of stomata.

The root suction pressure of roots of *Larrea* was in the example studied, more than three times that of privet roots.

A mature stem of *Larrea* offers almost twice the resistance to the passage of water under pressure, than that offered by a privet stem of the same length and same area of woody tissue.

In conclusion it might be suggested that the power of the protoplasm to endure desiccation and to recover from it unharmed, is the most effective "adaptation" of *Larrea* to a shortage of water.

I have pleasure in thanking Dr. F. Shreve for his kind help and criticism, and the Carnegie Institution for putting the resources of the Desert Laboratory at my disposal.

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³ These observations were made in February and March. In summer the creosote bush loses many of its leaves.

ROOT NODULES OF PODOCARPUS *

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INTRODUCTION

Recently Saxton ('30) in a interesting paper outlined the principal features of an investigation into the organisms present in the root nodules of *Podocarpus latifolius* R. Br. (*P. Thunbergii* Hook).¹ It seems that absence of bacteria and the presence of endotrophic fungal hyphae, or mycorhiza, were established from investigation of histological preparations as well as from microbiological cultures. The root material was collected from natural habitats (Table Mountain), *wherein no leguminous plants occurred for a considerable distance*. I stress this point, as Saxton ('30, 325) has suggested that certainly possibly, and perhaps probably, leguminous root nodule bacteria were absent from the natural habitats of *Podocarpus latifolius*, and of *Pherosphaera* which he also examined.

It is scarcely necessary for me to record that E. R. Spratt ('12),² in her investigation of the nodules of all but two of the genera of the Podocarpaceae, established by histological and cultural methods the consistent presence of *Pseudomonas radicicola* (Beijk.) Moore—universally associated with nodules on the roots of the Leguminosae. Her findings were supported as regards two Australian species of *Podocarpus* by McLuckie ('23), who also reported presence of mycorhiza in certain nodules.

In my monograph (Phillips, '31) on the ecology of the Knysna Forests, South Africa, I very briefly touched upon the fact that in 1922 I established the presence of *Pseudomonas radicicola* in the nodules of *P. latifolius* R. Br., and outlined the results of certain investigations with bacterial and seedling cultures.

The results of Spratt, McLuckie, and myself are opposed to the classic findings of Nobbe and Hiltner ('99), who described the presence of endotrophic mycorhiza only, in Podocarpean nodules,³ except that Spratt and myself did find occasional fungal hyphae in the outer, empty cortical cells—

* Abstract in S. A. Journal Science, 1931.

¹ Owing to the confused state of the nomenclature of *Podocarpus* I am forced to cite both incorrect and correct specific names, as well as authorities.

² See also Spratt, E. R., 1919.

³ Shibata (1902) in two Japanese species of *Podocarpus* found fungal mycelium, and extracted proteolytic enzymes from these; he recorded no bacteria. According to Rayner ('27, 194), Yeates ('24) found bacteria similar to those figured by Spratt and McLuckie, in 1 per cent only, of some hundreds of nodules from New Zealand *Podocarpus*.

the successive layers of collapsed tissue that surround the new cortical cells of the nodule season by season.

Saxton's work thus reopens the general subject of the organisms actually responsible for the development of the nodules, for he suggests that where *Rhizobium radicicola*⁴ is abundant in soils, it may conceivably "very readily obtain a footing immediately following the mycorrhizal invasion, and may even succeed in altogether supplanting the fungus hyphae in the soft, central tissue of the nodule," (italics mine). Further, he considers it possible that had Spratt worked with material from its original home, she might have obtained different results.

As the matter of the nature of the causal organisms in primitive habitats of *Podocarpus* is not of academic interest alone, but also of direct ecological importance, and not without meaning for the sylviculturist interested in the propagation of species of *Podocarpus* in original and new habitats, I venture to record briefly my own experiences with the nodules of several African species of *Podocarpus*, at the same time adding appreciably to the information given in my work already cited.

OBSERVATIONS AND EXPERIMENTS

During 1922-1925, I carried out in the Knysna forests—wherein *Podocarpus falcatus* R. Br., "Outeniqua," and *P. latifolius* R. Br., "Upright or Real Yellow-wood," are most important constituents—a series of observations and experiments; these, together with the results yielded are described.

The comparison of material from forest and other sites, *without* and *with* associated leguminous species respectively, was entirely incidental, and not intended. Fortunately the information yielded happens to have direct bearing upon the point of the occurrence or non-occurrence of leguminous nodule bacteria, raised by Saxton.

I. MICROSCOPIC EXAMINATIONS

Material

(i) Nodules from young seedlings and adults from *dense, climax forest*, Deepwalls; within the primitive habitat no leguminous trees, shrubs, or herbs occur: *Podocarpus falcatus* R. Br. and *P. latifolius* R. Br.

(ii) Nodules from young, nursery-raised seedlings, grown in soil that formerly had carried a dense community of the leguminous *Virgilia capensis*, associated with which were *Psoralea*, *Crotalaria*, and *Podalyria* spp.: Deepwalls; *P. falcatus*, R. Br.; *P. latifolius* R. Br.; *P. henkelii* Stapf (*P. Thunbergii* var. *falcata* Sim); *P. elongatus* (Ait) L'Herit., "Breede River Yellow-wood"; *P. thunbergii* var. *angustifolia* Sim.

⁴ According to Marshall ('21, 410), Hiltner and Störmer divided the nodule-forming bacteria of the genus *Pseudomonas* into two groups, possessing according to these authors, well-defined morphological and physiological differences: *Rhizobium radicicola* comprising the organisms from lupines, serradella and soy-beans, *R. beyerinckii* all the other forms.

(iii) Roots of seedlings grown in *sterile* soil and in control *normal* soil, mentioned under III, below; *P. falcatus* R. Br., *P. latifolius* R. Br.

Methods

Selected nodules were well washed before their study was commenced.

All sections or crushed nodular-content specimens were examined under oil immersion objective, after they had been suitably fixed (absolute alcohol) and stained (with crushed material, Ziehl's carbol-fuchsin, or aniline gentian-violet; with sections, Heidenhain's iron-haematoxylin and gentian violet; or Ziehl's carbol-fuchsin). Harrison and Barlow's ('06) test for the organism was used, after using Gram's stain: amyl alcohol does not remove the aniline gentian-violet, whereas ethyl alcohol does so with rapidity.

Results

(i) In all nodules not showing layers of collapsed cortical cells (*i.e.*, nodules not more than one season old), no evidences of fungal hyphae nor spores were obtained. On the other hand, in a few instances, non-septate fungal mycelium was noted in the outer, older cortical cells; this refers to all species mentioned, whether material was from forest, margin of forest, nursery, or *control* seedling culture. In no instance were spores noted, nor any signs of sporulating bodies.

(ii) In all young and in all older nodules, whether taken from seedlings or adults, from primeval forest or other sites, it was easy to demonstrate the abundant presence of bacteria; these invariably showed the characteristics of *Pseudomonas radicicola*: (a) they possessed minute, spherical bodies that stained strongly; (b) ethyl alcohol removed the Gram's stain, whereas amyl alcohol did not.

The features exhibited by the bacteria and by the tissues of the nodule, as described by Spratt for *P. elongatus*, were repeated with slight variation in the material studied.

From microscopic examination I have no doubt that in the material seen, the bacteria were the cause of the nodular development, and not the occasional mycelial strands observed.

II. MICROBIOLOGICAL CULTURES

Material

Nodules from seedling and adult *P. falcatus* R. Br. and *P. latifolius* R. Br., climax forest, and old Virgilia nursery soil, Deepwalls.

Methods

Cultures were made in tube and petri dish, of Harrison and Barlow's wood-ashes-maltose-agar, according to the following details: 16 grams well-burned, sieved, ash of *Ocotea bullata* E. Mey. "Stinkwood," boiled for 2

minutes in 1000 cc. distilled water, then passed through a double filter; to 800 cc. filtrate were added 8 grams agar, 8 grams maltose; the whole was then dissolved by heat, and was filtered, tubed and sterilized in the usual manner. Clean nodules, after being washed in dilute mercuric chloride, were opened by a sterile scalpel; from the margins, in some instances, and from the centers in others, portions of the contents were removed to heated, distilled water, in a sterile watchglass; from this suspension slants were infected. These were incubated at 22° C. in some instances, and at room temperature (ranging from 18° to 22° C.) in others.

On development of bacterial colonies, specimens were removed for microscopic examination.

Results

(i) In all nodules examined, whether old or young, from climax forest or *Virgilia* nursery soil, colonies of bacteria were grown; better, more vigorous colonies were obtained when the nodular contents had been removed from the more central portions of the swellings. The colonies were identical with those of *Pseudomonas radicicola* (Beijk) Moore: showing the characteristic oily, translucent appearance of colonies of this organism, and exhibiting the characteristic response to ethyl and amyl alcohol after Gram's stain.

(ii) In one instance only was a mixed culture of bacteria and fungus obtained; this resulted from the use of contents from near the periphery of a nodule that had shown presence of some fungal hyphae in the outer cortical tissue. The fungus seemed similar to that seen in the nodule: non-septate; it did not form spores in culture.

It may be recorded here that at the same time I made cultures from the root nodules of the leguminous *Virgilia capensis* Lamk., "Keurboom," and obtained cultures *identical* in general appearance and reaction with those obtained from the nodules of *Podocarpus*.⁵

III. EXPERIMENTS WITH SEEDLING CULTURES AND BACTERIAL INFUSIONS

Nobbe and Hiltner ('99) found that seedlings of *Podocarpus* could not be grown for any length of time, nor at all successfully even for a short time, in the absence of the organism causing the nodules; this organism they, as we have seen, considered to be an endotrophic mycorrhizal fungus. On the other hand, they showed that seedlings possessing nodules could be grown vigorously for five years in poor, quartz sand, from which nitrogen was absent.

The experiments outlined aimed at throwing further light on the interrelations of *Pseudomonas radicicola*, nodule development, and growth-vigor in seedlings of *Podocarpus*.

⁵ In light of the existing uncertainty of the nature of the particular biological race of the *Pseudomonas*, I now regret that I did not attempt to infect *Podocarpus* seedling with the organisms from the *Virgilia*.

Material

Some hundreds of podocarpia of *P. falcatus* R. Br. and *P. latifolius* R. Br. were carefully selected from one and the same mother-tree in each instance; these were examined externally and by weight, as to probable viability; they were then very thoroughly washed in distilled, slightly warmed water and finally were immersed for .5 minute in very dilute mercuric chloride solution, or for several minutes in dilute permanganate of potash solution; in the instance of *P. falcatus* the fleshy covering was removed before washing and sterilization, and in that of *P. latifolius* the "seed" was freed from the fleshy receptacle.

Methods

About three months before the experiments were commenced, I sterilized sharp, river sand, almost entirely non-organic in content, and ordinary forest loam with high organic content.

The methods employed with different samples of sand and loam were: (a) heating to 200° C. for several hours, and keeping the sterilized material within closed tins in the laboratory; (b) adding larger volumes of laboratory-quality methylated spirit to the material, allowing the alcohol to evaporate in air, then keeping the sterilized material in successive lots of clean boiled water for some months; to remove any possibly poisonous products.

After the podocarpia had been sterilized, they were sown in receptacles (9 x 11 x 9 inches) containing either sharp, sterile sand, or sterile loam; the sterile sand and soil vessels were kept away from all sources of infection. Control series of sand and loam receptacles were sown with podocarpia, and these were subjected to the same general conditions as experienced by the sterile series. Watering was done with boiled water in both series; separate watering vessels were used, to obviate any contamination by possible contact of the vessels with the normal soils.

Results

(i) Germination, on the whole, was equally good in the sterile and in the normal series, but the rate of development of the very young seedling was more rapid in the normal. Examination of very young roots and root-hairs from plants in sterile and control series alike showed that in the sterile series no bacteria had entered the root-hairs or other portions of the roots, whereas in the normal series there was an invasion of many root-hairs very soon after the development of the young roots.

(ii) Plants raised in sterile sand or loam grew slowly for several weeks, but ultimately died back slowly; plants in normal soil, plants showing nodules, at the same time were vigorous. In order to satisfy myself that: (a) the death of the cultures in sterile soil was not due to the toxic nature of the sterilized medium, (b) the cause of death actually was the absence of bacteria, I carried out the following simple experiments:

In one instance the contents of a nodule was ground fine upon a slide, then was washed into distilled water, and allowed to remain in this water for a few minutes; the suspension was then added to a vessel showing a number of poorly grown seedlings in sterile soil.

In another, the whole of a colony of bacteria was removed from a petri dish, was shaken up in distilled water, and then added to a second, poor culture of seedlings in sterile sand.

In both instances the seedlings showed incipient development of the nodules within ten days; in both cultures the majority of the seedlings recovered, and ultimately grew into relatively good plants.

(iii) Microscopic examination of the nodules formed in the sterile cultures after the addition of infusions of *Pseudomonas radicicola* showed the presence of the usual anatomical and bacterial characteristics of *Pseudomonas* nodules.

CONCLUSIONS

Bacteria either identical with, or very closely allied to, normal *Pseudomonas radicicola* were found in nodules from habitats *without*, and *with* leguminous plants. The occurrence of fungal mycelium was confined to the outer, usually semi-collapsed cortical tissues. Fungus was not found in young nodules. Seedlings without nodules were non-thrifty, and succumbed, unless watered with an infusion of *Pseudomonas radicicola* from Podocarpean nodules.

From the foregoing circumstances, I conclude that in the material examined the organism of importance was *P. radicicola*, and not the occasional fungal mycelium. While I examined a fair number of nodules, from some dozens of plants in two distinct primitive forest habitats, I do not affirm that extensive investigation of nodules from a large number of primitive habitats necessarily would return identical results. This phase of the problem is worthy of the attention of South African botanists suitably situated. If the outcome of Saxton's work and of this present paper should be the comprehensive study of material from primitive habitats, then some good will have been accomplished by the publication of these apparently discordant results.

This is essentially a problem where satisfactory results are obtainable only through collaboration of bacteriologist and ecologist or forester.

SUMMARY

(1) Saxton in a recent paper states he found no bacteria in the nodules of *Podocarpus latifolius* R. Br. from a primitive habitat, in which no leguminous plants grew. He considers it possible that the mycorrhiza recorded by Noble and Hiltner ('99) and himself may be the cause of the nodular growths on the roots of *Podocarpus*, and that *Pseudomonas radicicola* may be an invader from soil rich in this organism. His results also are in accordance with those of Shibata ('02) and Yeates ('24), but are discordant with those of Spratt ('12), McLuckie ('23) in part, and Phillips ('31).

(2) Material from the four South African species of *Podocarpus* examined microscopically, and from two species examined in culture by myself, showed presence of *Pseudomonas radicicola*. Such fungal mycelium as appeared in certain nodules only was confined to the outer older cortical tissues of nodules more than a season old, and was not found in young nodules.

(3) Seedlings of two species of *Podocarpus* grown in sterilized soil without nodules were non-thrifty, and succumbed, while controls possessing nodules lived. The watering of seedlings in sterilized soil and lacking nodules, with an infusion of bacteria from Podocarpean nodules or from cultures of *P. radicicola* grown from such nodules, enabled the plants to form nodules, and to grow relatively vigorously.

(4) *Pseudomonas* was present in nodules from primitive habitats lacking in Leguminosae, as well as in those from soil rich in leguminous nodule bacteria.

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REVIEWS

INTRODUCTION TO THE LITERATURE OF VERTEBRATE ZOOLOGY¹

We have, in Wood's recent compilation, more than a mere list of titles in the field of vertebrate zoology as found in the libraries of McGill University. Such a catalogue, alone, is an important contribution to zoological science, for the Blacker and other libraries of McGill are very rich, particularly in material of value to the historian of science. The compiler has furnished us in addition with a general review of this field of literature, a review in which various phases are considered separately. The value of the catalogue is enhanced greatly by this readable first section.

The work as a whole is divided into three parts. The first of these is the "Introduction" proper, consisting of a series of nineteen chapters, covering nearly one hundred and fifty pages. The approach in these chapters is historical, either explicit or implied. Only through such an approach can the selected materials be properly evaluated and coordinated. The historical method is supplemented for much of the material, particularly that of the last two centuries, by a division into subjects. This division is not altogether satisfactory, particularly for the ecologist. Although the literature of vertebrate zoology is full of ecological observations, here the only definite discussion of this field of vertebrate zoology is limited to a short paragraph in Chapter XIV, this chapter bearing the title, "The Literature of Zoogeography—Vertebrate Ecology—Vertebrate Paleontology—Animal Psychology—Zoological Gardens, Museums, and Stations." The ecologist can find reference to much of value to him, however, in all the other chapters as well. To the reviewer, one of the most interesting and illuminating of these is Chapter V, which is given over to a review of the literature of reports of scientific cruises, travels of naturalists, and related material.

The second section of the work is a short-title index arranged geographically and—under each geographic division—chronologically. This is a convenient means of locating lists of the vertebrates of particular regions, but it is, naturally, incomplete.

The third section is the catalogue proper, with the titles arranged chronologically under the name of each author. The book as a whole is based on the volumes in the Blacker Library of Zoology, the Emma Shearer Wood Library of Ornithology, the Osler Library, and the general library of McGill University. The third section is the catalogue of these titles, and is, therefore, only a beginning in the field. The compiler claims no more, but it is

¹ Wood, Casey A. 1931. An introduction to the literature of vertebrate zoology. 4 to, Pp. xix + 643. Col. frontispiece. Oxford University Press, London. Price, \$15.00 or 3 guineas.

a large beginning, certainly. Also catalogued are collections of animal drawings and paintings, and manuscript letters of naturalists.

The catalogue is incomplete to the extent that many papers (thousands) not being bound are not here catalogued and yet are available either as separates or bound in the journals possessed by these various libraries. Limited space made this omission necessary. The catalogue is therefore, to that extent, not complete for the libraries included. This deficiency is pointed out by the compiler. The journals (an extensive list of them) are named in the catalogue, and the annotations indicate in each case the degree of completeness of the files.

In spite of the limitations indicated, the volume will be found a very important reference work for all who are interested in the literature of vertebrate taxonomy or vertebrate faunas. The price makes it out of the range of the average individual worker, but it should be made available in all zoology working libraries.

GORDON ALEXANDER

UNIVERSITY OF COLORADO,
BOULDER, COLORADO.

INDICATOR SIGNIFICANCE OF BRUSH LANDS FOR THE GROWTH OF WESTERN YELLOW PINE

A study of unusual interest and significance in the application of ecological principles to the solution of an economic problem has recently been completed.¹ It deals with the causes for the absence of western yellow pine in brush vegetation of various types that occur throughout the mountainous portions of northern Utah, eastern Idaho, and western Wyoming, and, in fact, form a much interrupted and fragmented belt whose center extends from the Gulf of California to west-central Montana. Many of these brush sites, especially in northern Utah and southern Idaho, lie immediately below the Douglas fir type (which is continuous) and would normally be expected to support yellow pine, since they have the same elevation as pine clad areas in other parts of the West. An attempt to improve the brush cover by the planting of pines during a 5-year period ended in failure and led to the present investigations. They were conducted with the idea of determining the feasibility of planting pines, and thus extending the natural range of the forest, and of discovering means whereby areas suitable for the growth of pine could be determined.

A study was made to determine the characteristics of climate and soil in the brush lands, especially those lying between northern Utah and southeastern Idaho, and to compare them with conditions prevailing where the pines grew naturally. Temperature, although a potent factor in determining distribution

¹ Baker, F. S., and C. F. Korstian, 1931. Suitability of brush lands in the intermountain region for the growth of natural or planted western yellow pine forests. *U. S. Dept. Agri. Tech. Bull.*, 256.

of species in mountainous regions, does not explain the peculiarities of the pine on both sides of the brush-land belt. There is apparently a broad zone extending from the base of the near-by forested mountains to intermediate elevations covered with brush. Nor are there notable differences in total annual precipitation, which obviously is not the controlling factor in the plant distribution. The distribution of the precipitation during the summer months in the brush lands is, however, very different from that either to the north or the south. "May precipitation within the temperature zone suited to western yellow pine is ample for the reproduction of this species. In the pinelands to the south, the July and August precipitation, which greatly exceeds that in the brush lands, is ample for the reproduction of western yellow pine. In the intervening brush lands the light character and brief duration of May rain, coupled with the extremely dry June that quickly follows, prevents the establishment of the reproduction in the early spring. Deficiencies in July and August precipitation, combined with the fact that the rainfall usually culminates in August shortly before the early autumn frosts occur, make it impossible for the species to reproduce."

Although the distribution of the rainfall determines the general limits of the pine lands, the details of its boundaries are chiefly the results of local differences in soils. In general, the lighter types of soil are more favorable to the pines and especially so near the edge of their range, the pines spreading far from the main bodies of forest on sandy soils and along streams. The brush lands, in general, are characterized by calcareous, heavy, fine-grained soils and are prevailingly unsuitable for the growth of the pine. Unfortunately, data on climatic and edaphic factors in the brush lands and forests of this vast area are meager, but those available are convincingly presented.

In a second line of study, seedlings of the pine were transplanted under different conditions in the brush-land areas, since it is well known that planted stands often develop normally in regions where natural regeneration is impossible. Plantations were established in the brush belt in central, western, and northern Utah and also in southern Idaho. The effects on the transplants of soil moisture, soil texture, rate of evaporation, and shade were all carefully considered as well as injury by rabbits.

It was concluded that the establishment of artificial stands by planting is rendered extremely difficult by the same factors of rainfall that operate so powerfully against the natural reproduction of this species that the pine can not naturally invade the permanent brush lands. In fact, success in planting generally occurred only on sites with unusually favorable water content, and conspicuous success was attained only in seasons of exceptionally heavy spring rainfall. Moreover, suitable sites are not easily selected in average years, for they generally bear such a luxuriant cover of brush that failure of the seedlings due to shade is almost certain.

Attention was thus naturally directed to the use of the various native shrubs as indicators of desirable planting sites. Their natural succession,

root development, and leaf characters were extensively studied. A brief statement of the succession on wet and dry lands, and also the effect of fire is given. It is emphasized that the brush lands are the climatic climax and not subclimax vegetation resulting from repeated fires. Excellent sketches of the root systems of the pine and 21 of the most important shrubs are given, illustrating four general root types, *viz.*: deeply rooted species with taproots and practically no feeding roots in the upper layers; species with widely spreading rhizomes with a shallow network of roots and a deep-feeding root system; generalized root system; and 2-storied systems with practically no feeders in the intermediate soil layers.

In selecting planting sites not only soil moisture and root competition but also the degree of shade must be considered. A study of the vegetation on the ground enables all three factors to be evaluated with a fair degree of accuracy. The presence of shallow rooted species absorbing mainly in the surface soil indicates that the pines must be planted in direct competition with the native vegetation. Such sites are unsuitable for planting. "The best results can be obtained with plantations on sites where absorbing roots of the native vegetation are found at depths below 2 feet and where the trees can safely be placed close to the north side of the bushes where the shade will serve to reduce evaporation and transpiration. Such sites are likely to be naturally severe, as deep-feeding shrubs tend to occupy dry sites. Therefore, in most cases such sites should be selected for forest plantations only when they are otherwise naturally suitable." "If the native vegetation can be removed before planting, sites which originally supported a vegetation composed of shallow-rooted species will prove the most satisfactory. . . ."

The study of leaf characters included leaf size, structure, water content, relative transpiration, and sap density. These were made with the purpose of extending the usefulness of the native shrubs as indicators of planting sites by showing which deeply rooted species, as heavy users of water, may indicate areas where there is sufficient water available for western yellow pine. Although "there is no satisfactory way of summarizing all these factors so that their resultant effect is evident, for their relative importance is still largely unknown," yet with the aid of these criteria (including root characters and crown density) it is possible to select suitable sites for planting in the brush lands. A species should not be planted on any site where the native vegetation possesses uniformly higher sap densities than those generally maintained by the planted species during the dry season. "Contrary to an earlier belief, the brush lands are fundamentally unsuited to the natural reproduction of western yellow pine. . . . Moreover, there is no evidence that stands artificially established will maintain themselves or spread naturally as originally expected." "Only a portion of the brush lands can be classed as suitable planting sites, and the best sites, covered with deep-rooted, thin-foliaged shrubs on northern exposures, are rare." Cleared or burned sagebrush areas may show fair success; the remainder of the sites are inferior.

Hence, extensive planting in the permanent brush lands of the intermountain region is not justified.

This extensive research adds much to the ecology of the great intermountain region and is an excellent contribution to the important subject of plant indicators.

J. E. WEAVER

UNIVERSITY OF NEBRASKA,
LINCOLN, NEBR.

SOUTHERN WHITE CEDAR¹

This publication should be of interest not only to the forester but to the ecologist as well. It is composed of three principal parts. In the first part *Chamaecyparis thyoides* is discussed from every angle, including its characteristics and management as a timber tree. In the second part, the authors present a mass of much needed information concerning the economic importance of this little known species. The third part is of particular interest to the forester. Here are given yield, volume and taper and form tables. For the ecologist, however, the first eighteen pages are of particular interest. In these few pages the authors have succeeded in condensing a wealth of information. Condensed though it is, it is not presented in the form of a summary, and makes pleasant reading.

In the first part are included such topics as the distribution of this species in the United States, the climatic and edaphic conditions that control the distribution of the species and the biotic factors that influence the natural reproduction of the white cedar. It is of particular interest to note that birds and rodents consume but little of the seed crops and that reproduction depends largely on the proper conditions for the germination of the seeds and the survival of the seedlings. It seems that the main reason that this species does not cover larger areas is that its seeds are often imbedded in the litter and peat of the forest floor, where they remain dormant for long periods of time. Apparently it is the moisture content in the upper layers of the soil that serves as a controlling factor for the regeneration of this species. During the summer and early autumn many seedlings die for lack of moisture, while in the winter and spring, many seedlings are drowned because of prolonged flooding. Only on recent burns in water-filled swamps and on recently cut-over lands and clearings do the seedlings of the white cedar succeed in becoming established. Although the seedlings of this species can tolerate much shade, they are, nevertheless, frequently killed by the dense shade produced by the competing vegetation in the swamps. On cut-over areas, where the competitors have been removed, the white cedar seedlings come in dense stands often as many as 100,000 to the acre and sometimes even as many as 2,000,000 to the acre. On 8-year-old cuttings, as many as 30,000 seedlings to the acre were counted.

¹ Korstian, C. F., and W. D. Brush. 1931. Southern red cedar. U. S. Dept. Agri., Tech. Bull., 251: 76 pp.

Because of the excellent arrangement of the information and because of the wealth of data that it contains, I highly recommend this bulletin to foresters, ecologists, and botanists.

L. J. PESSIN

SOUTHERN FOREST EXPERIMENT STATION,
NEW ORLEANS, LA.

ECOLOGICAL LITERATURE RECEIVED

- Buxton, P. A.** 1931. The measurement and control of atmospheric humidity in relation to entomological problems. *Bull. Ent. Research*, **22**: 431-447.
- Rosendahl, Carl O., and F. K. Butters.** 1931. A guide to the spring flowers of Minnesota. xi + 89 pp. 25 pl. *Univ. Minn. Press, Minneapolis*. \$1.00.
- Dengler, Alfred.** 1930. Ökologie des Waldes, mit besonderer Berücksichtigung des deutschen Wirtschaftswaldes. vi + 272 pp. 118 fig. *Julius Springer, Berlin*.
- Keller, Paul.** Die postglaziale Entwicklungsgeschichte der Wälder von Norditalien. *Veröffen. Geobot. Inst. Rübel Zürich*, **9**: 195 pp. 38 fig. *Hans Huber, Bern-Berlin*.
- Beauverd, Gustave.** 1931. Recherches sur la flore vasculaire du massif de la Tournette. *Bull. Soc. Bot. Genève*, **23**: 1-418. 29 fig.

PROCEEDINGS

BUSINESS MEETING OF THE ECOLOGICAL SOCIETY OF AMERICA AT NEW ORLEANS, LOUISIANA, DECEMBER, 29, 1931

The Society met at 2:00 p.m. with President Weese in the chair.

REPORT OF THE REPRESENTATIVE ON THE COUNCIL OF THE UNION OF AMERICAN BIOLOGICAL SOCIETIES

Dr. W. C. Allee spoke of the necessity of the support of Biological Abstracts by the society and its members.

A motion was entertained and passed, *viz.*: That the matter of financial support of the Union of American Biological Societies be referred to the incoming executive committee with power to act.

A motion was entertained and passed, *viz.*: That the incoming president appoint two representatives of the society on the Council of the Union of American Biological Societies.

REPORT OF THE COMMITTEE FOR THE STUDY OF PLANT AND ANIMAL COMMUNITIES

Dr. V. E. Shelford proposed the following Policy for the Ecological Society of America, regarding **Preservation and Study of Natural Biotic Communities**.

Reports from the Advisory Board and other members of this committee¹ showed them unanimously in favor of nature sanctuaries to which only persons conducting scientific, artistic or literary work of a serious nature are to be admitted.² They believe that this is the only basis for the preservation of all the life (including carnivorous animals) of natural areas. The Committee does, however, hold that carnivores are very important in the economy of nature and should be left everywhere that their presence can be tolerated, after scientific investigation has shown their places in the biomicrocosm to which they belong.

The National Parks were especially stressed as suitable and desirable places for such sanctuaries, as a part of their function of preservation of the primitive. National Forests, State Parks, etc., are also favored. The Park Service, Forest Service, universities, special corporations, Department

¹ The five working representatives of other organizations agreed with the general principles. One seemed doubtful about sanctuaries in the National Parks.

² Nature sanctuaries should not be given publicity on account of the desire to visit them created thereby.

of Interior, Biological Survey, and State Conservation Commissions are mentioned as holding agencies, in the order given.

No legislation is necessary to establish nature sanctuaries in the National Parks, but some changes in the National Park policies may be necessary. Special legislation will be needed for the public domain, for nearly all state reservations, and probably also regarding the larger animals in the Natural Areas set aside by the Forest Service. Advisory commissions of scientific men are suggested as desirable for selection and supervision of the areas.

Nature sanctuaries must of necessity be evaluated and classified largely on the degree of modification of the primitive. There can be only a very limited number of first-class sanctuaries, with all the large animals native to the area present. Each nature sanctuary should be large enough to exceed the home ranges of the larger carnivores and herbivores³ contained therein. It should be surrounded by a larger area of park, forest, or game preserve so that overflow of animals into the surrounding area will not constitute a nuisance or be endangered.

Observations and census operations would be the only scientific work carried on in the sanctuaries, and those causing minor modifications should be carried on just outside in the buffer area. All modifying *experiments* would be confined to the buffer area.⁴ Pest-control measures (to be undertaken on scientific advice) would be undertaken here also, and perhaps confined to the outer border of the buffer zone in the case of roaming animals.

The Committee is convinced that exhaustive systematic census studies of all the life of natural areas will throw important light on questions of evolution, adaptation, extinction, migration, and fluctuation in population. Fluctuations in numbers of plants and animals are the basis for much of the economic effort of biology and agriculture, and, therefore, such pure-science researches are basic agricultural and "wild life" studies.

V. E. SHELFORD, *Chairman*

A motion was entertained and passed, *viz.*: That the above proposal of the Committee for the Study of Plant and Animal Communities be adopted and the committee commended for its work.

A motion was entertained and passed, *viz.*: That the incoming president is requested to appoint a Committee on the Preservation of Natural Conditions for Canada to be composed of the following: Dr. J. R. Dymond (*chairman*), H. G. Crawford, W. P. Fraser and Geo. J. Spencer.

A motion was entertained and passed, *viz.*: That the society grant monies from the treasury equal to those of 1931 (\$200 from the general fund, royalties from the sale of The Naturalists' Guide, and receipts from contributing members and societies).

³ This cannot be done for the more migratory herbivores.

⁴ Where this is National Park, the experiments would be made outside the park area.

REPORT OF THE COMMITTEE ON THE PRESERVATION OF NATURAL CONDITIONS

The following resolution was presented and approved:

Whereas, the unreserved and unappropriated lands of the public domain constitute an empire even yet containing resources in lands, minerals, plant and animal life of inestimable value; and

Whereas, a number of proposals have been made in various State Legislatures and the National Congress for modifying the present status of said public domain; and

Whereas, there is sometimes a tendency to omit or overlook certain important assets, as, for example, the generous resources in wild game life still characteristic of portions of this area, resources embracing not only a variety of less conspicuous game species, but also a considerable quantity of big game animals of unusual interest; therefore

Be it resolved, that the Ecological Society of America suggests that the fullest consideration be given to the problem of comprehensive scientific management of all natural resources of the public domain as a complete unit, including soils, waters, plant and animal life, and that there be adopted an adequate program of management including the following:

1. Periodic inventories of resources involved.
2. Studies of conditions of maintenance of these resources at their maximum productivity on a sustained yield basis.
3. Establishment of suitable natural areas for comparison and study.
4. Wise administration of all resources, so as to insure the greatest good to the greatest number over the longest period of time; and be it further

Resolved, that in view of the importance of the scientific approach indicated, not only from the standpoint of the agricultural, but also of the scientific and especially recreational and inspirational values involved, we earnestly urge that in every bill proposed or act passed, specific provision be made for the study and administration of watershed, grazing resources, and wild life.

V. E. SHELFORD, *Chairman*

REPORT OF THE TRUSTEE OF THE NATIONAL PARKS ASSOCIATION REPRESENTING THE ECOLOGICAL SOCIETY

The Trustee of the National Parks Association representing the society has attended one meeting of trustees in Washington and has provided the Association with material relative to the preservation of the primitive in animal life as a member of a committee on the "Preservation of the Primitive" of the Association.

V. E. SHELFORD

REPORT OF THE COMMITTEE ON NOMENCLATURE

The following report was read by Dr. W. P. Taylor:

The Committee on Nomenclature authorized at the Cleveland meeting on January 1, 1931 presents herewith the report for the year just closing:

The duties of the Committee were defined as follows:

1. To ask that members report to the Committee any terms which seem to need interpretation or clarifying.

2. To group these terms according to the types of workers chiefly using them.

3. To send these lists to the groups interested for discussion and return with comment and criticism.

4. To edit the replies from the groups and send all members of the society the complete list indicating the meanings which seem to have preponderance of support with comment of the Committee.

On account of the wide geographical separation of the members of the Committee, considerable time was consumed in its organization and in communications necessary to its operation. Consequently the requests for lists of terms from members of the society could not be sent out at a time favorable for attracting attention. As a result the Committee has been able to accomplish little toward performance of items 2, 3, and 4 of the above mentioned duties. That this failure is due to circumstances rather than to indifference of the members of the society is indicated by the fact that a number of members of the society have shown active interest when conversing with members of the Committee. It seems probable that these and many other persons might be more responsive to individual letters than they have been to the circular letter containing the request of the Committee which was printed in the Bulletin of the Ecological Society for June 1931.

As matters stand it seems that the Committee can do no more toward recommendation as to usage of terms than to present the short list now in hand with a suggestion as to lines of general classification which may be represented in it and by it.

1. **Habitats.** Swamp, Marsh, Coincidence, Mesic, Xeric, Hydric.

2. **Combinations of influences.** Coincidence.

3. **Items of influence.** Condition, Factor, Influence.

4. **Changing influence.** Variable, Fluctuant.

5. **Control of influence.** Inhibit, Stop, Retard, Introduce, Augment, Sustain.

6. **Degree of influence.** Maximum, Minimum, Optimum.

7. **Character of observation.** Ascertain, Determine.

8. **Direction of influence.** Increase and decrease, Rise and fall, Ascending and descending, Systole and diastole, Wax and wane, Ebb and flow.

9. Group of unrelated organisms of similar influence. Forb, Weed.

Respectfully submitted,

H. C. HANSON
 J. G. NEEDHAM
 W. P. TAYLOR
 A. G. VESTAL
 W. E. ALLEN, *Chairman*

A motion was entertained and passed, *viz.*: That the report of the Committee on Nomenclature be accepted and referred to the incoming executive committee with power to act. It was suggested that a Committee on Nomenclature be continued.

REPORT OF THE SECRETARY-TREASURER

The report of the Secretary-Treasurer was presented and approved as follows:

Receipts under A. O. Weese

Balance on hand, December 1, 1930	\$ 1,849.62
Refund from A. O. Weese80
Dues	
1930 dues	\$ 4.20
1931 dues	130.00
Sustaining (1931)	24.00 158.20
Total receipts, January 1, 1931	
	\$2,008.62

Disbursements under A. O. Weese

Ecology (memberships)	\$ 466.20
Ecological Monographs (memberships)	100.00
Printing	75.00
Expenses of secretary, Cleveland	105.31
Total disbursements Dec. 1, 1930-Jan. 1, 1931	
	\$ 746.51

Balance turned over to A. E. Emerson \$1,262.11

Receipts under A. E. Emerson

Balance on hand, January 1, 1931	\$1,262.11
Dues	
Current (1931)	\$1,675.14
Advance (1932)	294.00
Arrears	8.40
Life	200.00
Sustaining (1931)	470.20
Sustaining (1932)	72.00
Contributing	9.00 2,728.74

Naturalists' Guide Royalty	23.50
Interest	44.56
Refund	7.00

Total receipts Jan. 1, 1931-Dec. 1, 1931 \$4,065.91

Disbursements under A. E. Emerson

Ecology (memberships)	\$1,267.00
Ecology (longer paper fund)	104.87
Ecological Monographs (memberships)	407.20
Investments	900.00
Secretary's Office	
Postage, Telegrams and Express	\$ 54.20
Clerical Assistance	119.17
Printing and Stationary	239.16
Expenses, Pasadena	7.00
Expenses, Washington	5.50
	425.03

Advertisement for Naturalists' Guide, Journ. Ecology	7.79
Committees on Preservation of Natural Conditions and the Study of Plant and Animal Communities	232.50
Committee on Land Utilization	6.00
Checks returned	8.25
	\$3,358.64
Balance on hand December 1, 1931	\$ 707.27

Total Assets, 1931

General Fund	
Cash on hand	\$ 617.30
Life Membership Fund	
Cash on hand	\$ 89.97
Securities	1,120.63
	1,210.60
	\$1,827.90

Membership, 1931

Sustaining Life	2
Life and Sustaining	2
Life	7
Sustaining Institutional	4
Sustaining	93
Institutional	3
Active	455
Contributing	3
Associate	26
	—
Total paid up	595
In arrears 1 year	47
	—
Total	642

ALFRED E. EMERSON,
Secretary-Treasurer

REPORT OF THE BUSINESS MANAGER OF ECOLOGY

The following report of the Business Manager of ECOLOGY was presented and approved:

For the Fiscal Year, December 1, 1930–November 30, 1931

Received

Cash on hand (statement of 1930)	\$ 204.00
Alfred Emerson, Treasurer, E. S. A.	1,727.30
Subscriptions, 1931	\$1,621.97
Subscriptions, 1932	209.23 1,831.20
Single Numbers and Back Volumes	222.79
Cost of Excess Pages	510.73
Paid by Authors for Excess Proof Corrections	30.11
Longer Paper Fund	104.87
Postage (H. De Forest and C. F. Adams, plus Archie Gibson (\$80 deposited)	1.30
National Academy of Science	500.00
Subsidy from Brooklyn Botanic Garden	500.00
Interest, June 1931, received from bank	2.01 \$5,634.31

Disbursed

Printing

Lancaster Press, Inc.

Reprints for Oct., 1930, and Jan., 1931	\$ 337.99
January, 1931, issue	1,352.08
April, 1931, issue	1,210.97
July, 1931, issue	1,031.01 \$3,932.05

Illustrating

National Engraving Co.

November and December, 1930	\$ 417.67
April, 1931	218.63
April 23 and 29 bills	134.43
October, 1931	81.94 852.67

Advertising

Office Expenses

Clerical Asst. for 12 mo. @ \$10.00	\$ 120.00
Stationary	41.80
Postage	53.50
Addressograph Stencils occasioned by changing form of mailing list	49.61
Expressage	3.68
Postage (H. De Forest and C. F. Adams)50 269.09

Miscellaneous

Collection Charge on Check10
Cash Balance on hand November 30, 1931	399.55 \$5,634.31

Examined and found correct.

H. P. SCHIOENBERNER

Auditor

Assets and Liabilities

December 1, 1930–November 30, 1931

Assets

Cash in Bank	\$399.55
Bills Receivable	
Back Volumes	\$ 20.00
Subscriptions, 1931	\$ 11.90
Subscriptions, 1932	193.38 205.28
Single Numbers	2.40 227.68
	<hr/>
	\$627.23

Liabilities

Bills Payable

Lancaster Press, Inc.,	
October, 1931, issue	\$840.81
National Engraving Co.	129.60 \$970.41

Liabilities over Assets	343.18 \$627.23
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Circulation Data as per Mailing List of October, 1931

1. Members	553
2. Subscribers	483
3. Exchanges	91
4. Advertisers	11
5. Editorial Office	2
	<hr/>
	1,140

Number of copies printed per issue	1,400
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C. STUART GAGER,
Business Manager of Ecology

A discussion followed concerning the financial status of ECOLOGY.

A motion was entertained and passed, *viz.*: That a vote of thanks be transmitted to C. S. Gager for his method of handling matters pertaining to ECOLOGY.

REPORT OF THE EDITOR OF ECOLOGICAL MONOGRAPHS

The following report was read and approved:

Gentlemen:

As editor of *Ecological Monographs* I have the honor to submit the following report for the year 1931.

Four numbers, which included 520 pages and 126 figures, were published. There were 200 subscribers.

Cost of Volume I	\$3,646.89
Received	
Subscriptions	\$1,306.84
Advertisements	120.00 1,426.84
Deficit	\$2,220.05

Yours respectfully,

A. S. PEARSE,
Editor of Ecological Monographs

REPORT OF THE NOMINATING COMMITTEE

The following resolution was submitted and approved:

Whereas, the diversity in the character of the papers submitted for publication in ECOLOGY makes it difficult for any one individual to pass judgment on all of them, and in order to relieve the editorial office of some of the work and delay heretofore involved in reaching a decision as to suitability of the papers submitted,

Be it resolved, that the office of Associate Editor be created, with a tenure of five years, coinciding with the term of office of the Editor, and that the men appointed to these offices be selected to represent as widely divergent aspects of ecological work as possible.

Election of Editorial Staff and Board

The following nominations for the editorial staff of ECOLOGY were approved and the men elected to fill the unexpired term of Barrington Moore (4 years), the editorship and associate editorship to run concurrently:

Editor, Alfred E. Emerson
Associate Editor, George D. Fuller

The following nominations for the editorial board of ECOLOGY were approved and the men elected for a three-year period to replace the members of the board of editors whose terms have expired (C. C. Adams, W. E. Ekblaw, Joseph Grinnell, S. A. Waksman):

A. O. Weese
A. S. VESTAL
C. T. Vorhies
Stanley Cain

The members of the board of editors who still have two years to serve are: G. E. Nichols, G. A. Pearson, E. B. Powers and J. G. Needham.

The members of the board of editors who still have one year to serve are: F. E. Lutz, Chancey Juday, J. E. Weaver and Forrest Shreve.

Election of Officers

Officers for 1932 were nominated and elected as follows:

President, George E. Nichols

Vice-President, Joseph Grinnell

Secretary-Treasurer, Raymond Kienholz

The meeting adjourned at 4:45 P.M.

ALFRED E. EMERSON,
Secretary

LETTER OF APPRECIATION TRANSMITTED TO BARRINGTON
MOORE

Mr. Barrington Moore,
Stone Acre,
Corfe, Taunton,
England.

Dear Mr. Moore,

At a business meeting of the Ecological Society at Tulane University on December 29 your resignation as Editor of ECOLOGY was transmitted by President Weese and accepted with universal expressions of regret.

On a motion made at that meeting the undersigned were appointed to draft this letter to you as an expression of the appreciation and gratitude of the Society for your long and valued services as the Editor of our official journal. Your broad sympathy with all lines of ecological work, your critical and discriminating selection of material for publication, the scholarly standards which you have maintained for the journal, and the cordial and sympathetic relations which you have steadfastly maintained with contributing members, have all served to inaugurate our principal journal on a plane of dignity and usefulness such as we hope it may long maintain.

You may be interested to learn that Dr. A. E. Emerson has been appointed Editor, and Dr. Geo. D. Fuller Associate Editor. It will give you some merited satisfaction to know that we now need two men to perform the duties that you have been fulfilling.

With all good wishes, we remain

Sincerely yours,

W. C. ALLEE
GEORGE E. NICHOLS
FORREST SHREVE

NOTES AND COMMENT

ANIMAL ECOLOGY DEFINED?

In a recent biological publication, there appear three papers dealing with the distribution of a marine species. These three papers do not agree in their findings, which I think is to be expected because they attempted to correlate this distribution with salinity as the controlling factor.

After reading the above accounts I noted on a slip of paper several factors that influence distribution, any one of which might be as potent as salinity. No doubt many more could be added.

If we were not so busy making complicated definitions as to what Ecology really means, but were to accept a simple one such as Elton's "Ecology is simply scientific Natural History," or "Ecology is the study of an organism in relation to its environment," we would then realize that a unit factor is but a tree of the forest. We are turning the subject upside down, unit factor problems vs. complicated definitions. Particular problems in ecology may be complicated enough to suit any one with a fancy for complexity.

Ecology, when simply defined, fits so nicely into the scheme of biological investigation that it seems difficult to propose a reason for complicating it. If we divide zoology into three main groups we have morphology, physiology and ecology. This may seem presumptuous to some. Yet, if we but consider what biology means, certainly none will contend that the study of the living animal is less important than the study of one of its parts. A deer has four legs, a morphological fact; it uses them for locomotion, a physiological fact; it uses them to carry itself to food, out of danger or to a mate, ecological facts. Morphology and physiology deal with the cell as the unit of structure and function. Ecology deals with the organism as a whole. Ecology is no more separated from either morphology or physiology than they are from each other. What a fine picture we would have of an animal were a morphologist, a physiologist, and an ecologist to "do one" together. That Ecology completes the picture justifies the simple definition and will give to Ecology a permanent place in the scheme of zoological study, which complicated definitions and laboratories will not.

I really cannot see that it makes a great deal of difference whether we start with a single animal or with the community itself when conducting an ecological study, for no one can study an individual species in conformity with the definition that "Ecology is the study of an organism in relation to its environment" without studying the community.

A definition for environment in Webster's Unabridged Dictionary states that it is the "aggregate of all the external factors affecting an organism."

Personally, I like to begin an ecological study by viewing the community; however, it is only after I have learned intimately the life histories of a few of the more prominent members that I really begin to understand the community as a whole.

Possibly our incentive to use unit factors comes from obvious effects of limiting factors. If, however, we remember that any factor becomes a limiting factor when carried to an extreme, we will not be so likely to try building an environment with a unit factor.

Ecology is a field science. The principle of variation alone indicates that one cannot understand animals and animal communities unless the major portion of the study is carried on in the field, especially in view of the fact that habits and instincts are a

response to the environment, and, therefore, are as important in an evolutionary sense as are morphological structures or physiological functions. Not one of the three can be correctly interpreted and used as background for natural laws unless the interpretation is founded on field study, or, in other words, the study directly of the fitness of the animal for its environment. A laboratory is only a place in which to check conveniently certain problems which arise in the field. A laboratory environment is not a natural environment and laboratory studies are always subject to this qualification. If an environment is the *sum total* of all external factors, then varying one factor changes the summation and therefore the entire environment.

I sometimes wonder if such splendid results as, for example, Elton or Grinnell obtain, are not due to the fact that larger animals do not "fit" in a laboratory. These men therefore are field ecologists.

CONCLUSIONS

1. A simple definition of ecology will put it on a permanent foundation which will round out the field of zoology.
2. It will give ecologists a place of sympathetic understanding within the zoological personnel.
3. The results will be more comprehensive and lead to a better understanding of the principles concerned with life, and, therefore, of life itself.

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USE OF THE QUADRAT IN STUDYING THE PLANT-CUTTING ACTIVITIES OF THE ANT, *Pogonomyrmex occidentalis*

The ant, *Pogonomyrmex occidentalis* Cr., constructs cone-shaped mounds throughout the plains and semi-desert regions of the western United States.¹ Each mound, in its more or less mature condition, is surrounded by a circular area from which the vegetation has been removed by the ants. These circular, vegetationless regions are generally referred to as "cleared" or "denuded" areas. The rapidity with which the denuded area is established is apparently dependent upon the numerical strength of the colony, the amount of adjoining vegetation and the prevailing climatic conditions.

On June 18, 1931, a normal, incipient mound 32 cm. in diameter was selected in a region of representative vegetation near Twin Falls, Idaho. With cloth tape a quadrat 10 m.² was laid out in such a position that the formicary was located as nearly in the center of the square as possible. A list and chart were then made (table I and fig. 1).

TABLE I. *The plant population of the quadrat before and after denudation*

Plants ²	Individuals present June 18	Individuals present	
		September 14	
<i>Aster</i> sp.....	3		3
<i>Agropyron repens</i> (L.) Beauv.....	18		18
<i>Chrysothamnus graveolens glabrata</i> (Gray) A. Nels.	2		2
<i>Artemisia tridentata</i> Nutt.....	1		1
<i>Bromus tectorum</i> L.....	3819		3704
<i>Salsola pestifer</i> A. Nels.....	2502		2137

On September 14, 1931, the quadrat was again visited and another list and chart made (table I and fig. 1). By this time a denuded area had been established by the ants

¹ McCook, H. C. 1882. The honey ants of the Garden of the Gods, and the occident ants of the American Plains. *J. B. Lippincott & Co., Philadelphia.*

² Determinations by R. L. Piemeisel, Bureau of Plant Industry, U. S. Dept. of Agric., Twin Falls, Idaho.

and the mound had increased in size to 59 cm. in diameter. The areas of vegetation within the quadrat had remained practically the same but the plants immediately surrounding the mound, predominantly Russian thistle, had been cut by the ants. Approximately 365 plants of Russian thistle had been destroyed.

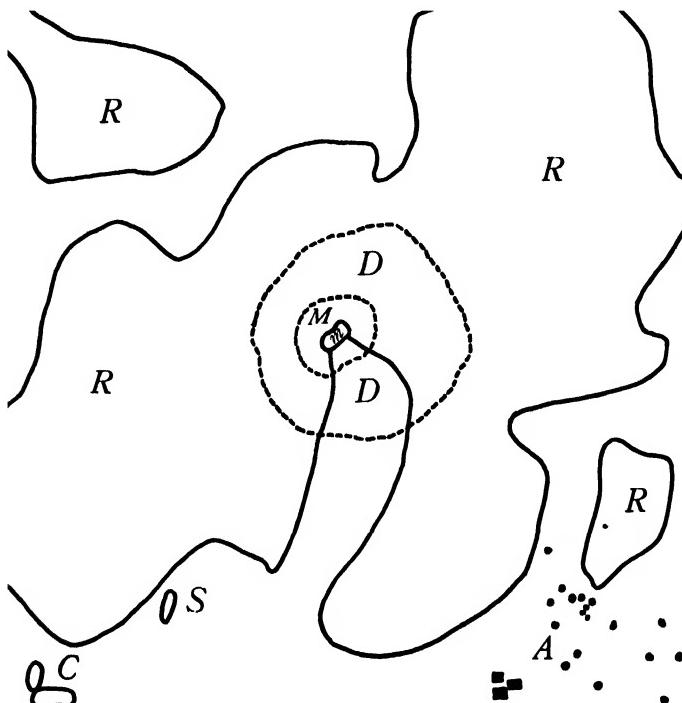


FIG. 1. Chart of the quadrat before and after denudation by *P. occidentalis*. Ant mound (*m*) before and (*M*) after denudation, (*D*) denuded area (broken outline), (*R*) Russian thistle, *Salsola pestifer*, (*C*) *Chrysanthemum glabratum*, (*S*) sage, *Artemisia tridentata*, (*A*) *Aster* sp. (the squares) and *Agropyron repens* (the dots). The remainder of the area is occupied by *Bromus tectorum*.

The quadrat seems to be a desirable unit to employ in the study of the destruction of vegetation by *P. occidentalis* during mound construction. Undoubtedly it could be used with advantage in the study of activities of other mound-building ants.

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A SIMPLE, INEXPENSIVE INSTRUMENT FOR THE MEASUREMENT OF LIGHT

In forestry, ecology, and other branches of science, the measurement of light as a factor of the environment often occasions considerable difficulty. This is due both to the excessive cost of refined light measuring instruments and to their cumbrousness which makes them difficult to transport and to use in the field. This paper points out the possibility of using a simple instrument, weighing about one pound, that can be made at a cost of but a few dollars.

The instrument here described was made and used by Graham ('22). It is based

upon the difference in radiation absorbed by a black and a white surface, light intensity being a function of the difference in temperatures observed. The instrument consists of two mercury thermometers mounted in a simple wooden frame or box about two inches apart and parallel (fig. 1). The bulb of one thermometer is blackened and the other whitened. Black Duco enamel may be used for the black thermometer and a white zinc oxide enamel for the white. The disadvantage of the Duco is that it gives a shiny finish but this can be overcome by using some lamp black mixed with insulating varnish. When mounted as shown, approximately the same conditions prevail for both thermometers. Thus the difference in temperature represents the differential in absorption rate.

The writer used this instrument for light measurement in conducting an ecological study in two forest habitats, a part of his graduate studies at the University of Michigan under the general guidance of Professor S. A. Graham of the School of Forestry and Conservation. Approximately simultaneous daily readings were taken in the two habitats under observation for the period from June 15 to September 1, in northern New England in 1929, and in northern Michigan in 1930.

During 1930, a Macbeth illuminometer was used in addition to the black and white thermometers, thus permitting a comparison of the instrument in question with a standard instrument for measuring light. The results obtained were very gratifying.

The Macbeth illuminometer, manufactured by Leeds & Northrup Company, is a very satisfactory instrument for the measurement of light for most purposes, although it is limited in that it is selective in character and measures only the visible spectrum. It, however, does give a very accurate measure of all intensities within the limits of human vision. The principle of the Macbeth illuminometer is the comparison of the light from a test plate with the intensity of light from a working standard lamp which may be moved nearer or farther from the eye as required to obtain an intensity match. Light is measured in foot candles with this instrument with a range from 0.02 to over 15,000-foot candles.

A comparison of almost simultaneous readings showed a very high degree of correlation between the results obtained. The relationship expressed by the correlation coefficient is $+ .9805 \pm .0039$. This appears to be very significant and is further substantiated by the arrangement of the paired observations on the correlation surface (fig. 2). The difference in temperature between the black and white thermometers was used as one variable and the foot candles as read from the Macbeth illuminometer as the other variable.

It is interesting to note in this relationship that a difference of 1° F. on the set of black and white thermometers used corresponded to a light intensity of about 1,000 foot candles. This relationship seems to vary directly and the regression line lies close to a line running at a 45-degree angle with the base when 1° F. on the abscissa equals 1,000 foot candles on the ordinate. An average difference of 1° F. is equal to average of 1,140 foot candles while a difference of 13° F. is equal to 12,480 foot candles. This would of course vary with each set of black and white thermometers.

It would appear from these data that the difference in temperature between the black and the white thermometers might be standardized against an instrument such as the Macbeth illuminometer in order to convert the readings directly into some universal unit of light measurement such as foot candles.

This would have a decided advantage over the methods hitherto used, which are to express light either on a percentage basis, taking the highest reading of the season as 100 per cent or in terms of the actual difference in degrees.

The disadvantage of using the percentage basis for light measurements lies in the fact that the results of different seasons or regions do not lend themselves to ready comparison because of differences in the maximum readings obtained during different seasons or in different regions. However, this system is of value when two or more habitats are to be compared during any one season.

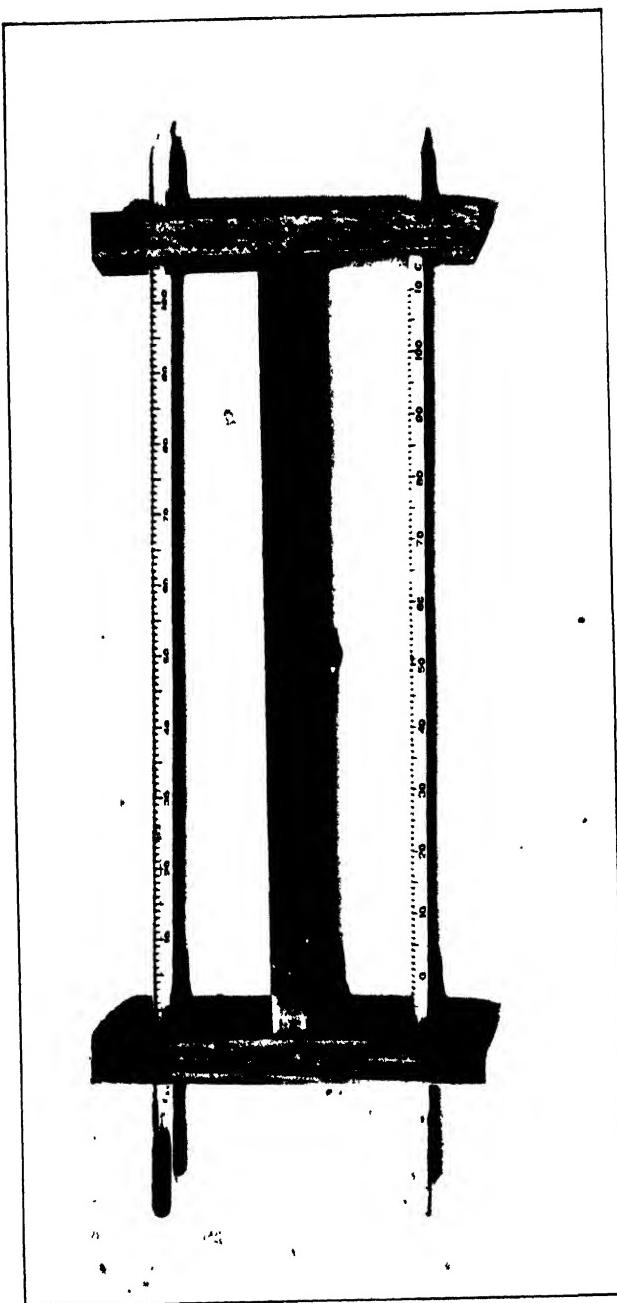


FIG. I. Instrument used to measure light.

The chief disadvantage in the use of the black and white thermometers for light measurements is in the range of low light intensity below 1,000 foot candles. The thermometers used in this study were graduated in single degrees and often no difference in temperature would be noted under the forest canopy, especially on cloudy days, although there probably would have been a slight difference observable if the graduations had been finer. By the use of thermometers which could be read to $1/10^{\circ}$ F. a very slight difference in temperature could be detected readily.

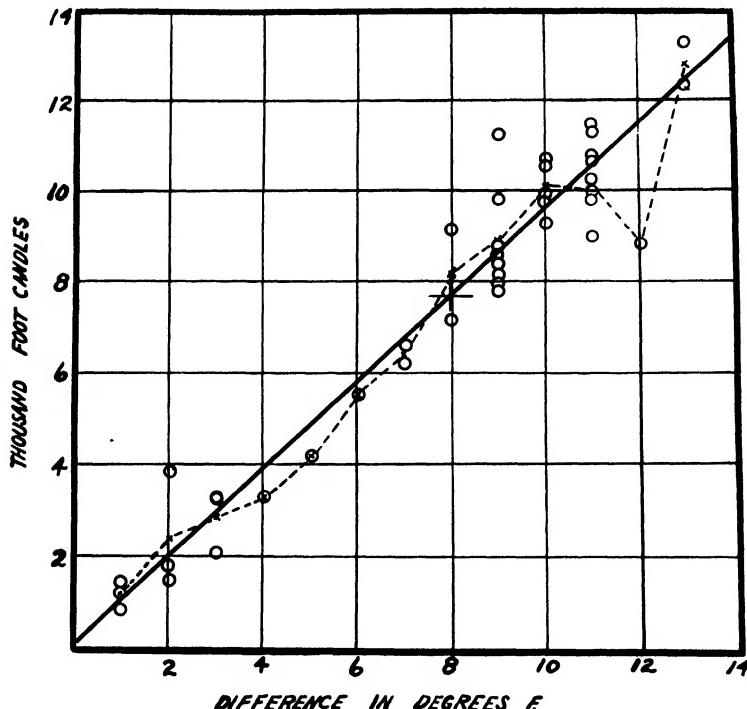


FIG. 2. Relationship between the difference in temperature between black and white thermometers and light intensity as measured in foot candles by a Macbeth illuminometer.

It would be interesting to check the black and white thermometers against some of the more refined instruments for measuring light, such as the Gast ('30) Spherical Hot-Junction Thermopile, the Coblenz ('14) type of thermopile, or the photoelectric cell (Coblenz, '28).

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A METHOD OF MAKING PERMANENT BLACK ATMOMETER BULBS¹

The common method of blackening Livingston atmometer bulbs by covering them with a paste of lampblack in distilled water has proved unsuccessful in the Hawaiian Islands during the rainy season, since the heavy tropical rains remove such a coating in a minute or two.

Since a supply of black bulbs was required for certain ecological studies on the Pineapple mealy bug *Pseudococcus brevipes* Ckll., the writer was asked to search for a method of making them. It was necessary to produce a permanent black, which would not increase the variability of the evaporative rate from the bulbs. The following technique has proved quite successful.

Immerse the dry white bulb very suddenly in a 3 N solution of chemically pure silver nitrate, leave three or four minutes, lift out and dry with a cloth. Then immerse equally suddenly in a developer solution made from one part of water to one part of "Nepera" solution, until the color ceases to darken.

Remove from this solution, wash briefly in distilled water, and re-immerse in the silver nitrate. Again remove, dry with the cloth and replace in the developer. This should give an absolutely jet black color.

The bulb is now washed under the tap, rubbing gently with a cloth meanwhile, and is then put to soak for about a week in numerous changes of distilled water until no more soluble silver salts can be leached out. These soluble silver salts may be readily detected by adding a drop of 1/10 N, sodium chloride to the wash water, a dense white cloudy precipitate showing the presence of silver.

If, owing to faulty washing, any of the bulbs fade, they can often be renewed by cooking for five minutes or so in hot nitric acid, one part concentrated acid to one part water, washing briefly and then re-developing.

It is essential that the immersions of the bulb be made with a single rapid motion, since slow immersion produces indelible "tide-marks" around the bulb.

It was found that bulbs made by this method gave excellent service, and were no more variable in their evaporative rates than new standardized white bulbs. As a matter of fact, the Coefficient of Variability for seven black bulbs over a period of ten days was only 2.735 per cent while the same constant for seven white bulbs over the same ten days was 3.104 per cent. The difference is probably not statistically significant.

Bulbs made by the above method have been in use for many months in the Islands without fading, but certain precautions must be observed in their use and manufacture. If the washing-out of the soluble silver salts is not most carefully done, the bulbs will certainly fade. Also, should it at any time be necessary to re-lacquer the stems of such bulbs, the bulbs should not be heated in an oven to dry the lacquer, as for some as yet unknown reason, such heated bulbs rapidly fade when again placed in the field. Care should also be taken in the matter of adding chemical substances to the water in the atmometers, to prevent algal growth. It must be remembered that the silver coating is colloidal in form and is thus highly reactive, and may form light colored or colorless compounds with the added chemical. However, minute quantities of organic substances such as hexylresorcinol seem to do no harm, but compounds of heavy metals such as mercury, lead, silver or chromium are particularly to be avoided. Owing to the chemical treatment the stems of these black bulbs are peculiarly liable to peel. They should therefore be frequently examined, since such peeling greatly increases the evaporation rate.

¹ Technical Paper No. 22 of the Association of Hawaiian Pineapple Canners, University of Hawaii.

Summary

A method of producing an unvarying constant black coloration in Livingston atmometer bulbs by the use of silver nitrate is set forth, and certain precautions to be observed in the manufacture and maintenance of such bulbs are outlined.

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LENGTH OF DAY IN RELATION TO THE NATURAL AND ARTIFICIAL DISTRIBUTION OF PLANTS

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The plant organism is a complex of many potentialities of expression. Certain requirements must be met before the plant can grow and produce seed successfully. In addition to demands for particular levels of temperature, soil moisture and various chemical associations, it has come to be recognized within recent years that definite length-of-day requirements must be met.

The plant is dynamic to the degree that it remains indigenous to a particular locality only from necessity. It is a potentiality of all organisms to invade new territory, and in this way life is given greater guarantee of survival. It is normal for all plants to scatter their progeny on the earth more or less indiscriminately, allowing wind, stream, bird, beast and man to do the widespread transplanting of the species. Wherever the seed may come to rest subsequent survival depends upon the physiological requirements of the seedling and the mature plant.

Length of day is a factor of the environment wherever plants grow. As conditions now obtain, a wide range of day lengths is found in the terrestrial plan from the equatorial regions to the poles. On the equator, the days and nights are nearly equal, making alternations of approximately 12 hours of daylight and darkness. Beyond the equator, there is a progressive daily change toward long days in spring, culminating in the longest days of the summer at the summer solstice around June 21. With the passing of the summer solstice, the days progressively decrease in length through the autumn until the shortest days are attained at the winter solstice around December 21. At the equinoxes, March 21 and September 21, a world-wide equalization of daylight and darkness obtains briefly in the ceaseless seasonal progressions.

Passing along any line of longitude from the equator to the poles at the summer solstice, we find the daylight relations changing from 12 hours of maximum illumination, to culminate finally near 66° with continuous illumination, there being no actual night here during the growing season. In other words at every latitude, a certain maximum length of day obtains in summer, increasing with increase in latitude, until at about 66° the sun remains in the

skies during the entire 24-hour period. An exact reversal of these conditions obtains at the winter solstice, the far northern regions for months having no sunlight, with a progressive decrease in the hours of night from latitude to latitude southward until close to 12 hours of night and, naturally, 12 hours of day are again experienced at the equator.

These fixed and striking seasonal relations in the terrestrial day length of various latitudes involve other conditions which the plants must meet. It has been pointed out that at the equinoxes about March 21 and September 21, the days and the nights become equal, that is, about 12 hours the world over. Since the maximum length of the midsummer day at the solstice increases progressively with each step up in latitude from the equator, it is obvious that the greatest total change from the maximum length of the midsummer day to the day-length conditions of the equinoxes must take place at the highest latitudes. At high latitudes this change amounts to large daily or weekly increments in spring until the summer solstice is reached. Conversely, when the midsummer days are passed, there are corresponding decrements until the equinoxes are reached, and thence onward until the winter solstice period is attained. To understand these seasonal relations, a specific instance may be mentioned. At 60° the total change from the vernal equinox to the summer solstice, that is, from day-length conditions ranging from 12 hours to 18 hours 36 minutes, amounts to 6 hours and 15 minutes. The total change for the same period of time at latitude 23° is only 1 hour 22 minutes. During the growing season, then, relatively very rapid increments and decrements in length of day distinguish the higher latitudes from the lower latitudes. Furthermore, the mean length of day is much greater during the growing season at the higher latitudes.

The subject may now be approached from the standpoint of invading plants in relation to these terrestrial features of length of day and its seasonal changes. Tests have shown that plants vary greatly in their length-of-day requirements, some flowering only when the length of day is near or below 12 hours. These have been termed short-day plants, because flowering is initiated in nature on a shortening length of day. The poinsettia and late varieties of chrysanthemum are typical examples. Other plants flower only on an increasing length of day somewhere in excess of 12 hours. These constitute the long-day types of plants, typical of which are certain strains of timothy, golden glow, wild senna, *Cassia marilandica* and some species of garden stonecrop such as *Sedum telephium*. Many other plants seem not to fall into either group, but flower with little difficulty under the longest or shortest lengths of day. These have been looked upon as indeterminate types in their flowering behavior, for thus they seem to be with respect to the natural terrestrial lengths of day found from the equator throughout the temperate zones. Among these are such plants as common purslane, *Portulaca oleracea*, the garden *Portulaca grandiflora*, and the tomato of our gardens.

Taking a plant, then, from one region to another northward or southward of its normal habitat may result in very different behaviors. A typical long-day plant native to Canada, whose flowering is initiated on an increasing length of day may fail to flower when introduced southward where the critical length of day capable of inducing flowering is never attained, or is maintained too briefly to promote flowering. The garden stonecrop, *Sedum telephium*, shows this behavior in a striking manner. This sedum is a garden ornamental, flowering successfully in the latitude of southern Vermont. When grown at Washington, D. C., it remains strictly vegetative, producing flowerless stems only. The same behavior is shown under all lengths of day of shorter duration. With the addition of artificial light from sunset till midnight in winter time, thereby increasing the daily illumination to a mean value of something more than 15 hours, the plants have been readily induced to flower.

During the summer of 1931 these plants were grown under constant lengths of daily illumination by the use of artificial light afforded at sunset. This necessitated adjustments in the use of the artificial light as the natural length of day itself increased in order to secure a constant daily illumination. In these tests, beginning April 11, daily illumination of 15, 16, 17 and 18 hours was maintained. The control plants, as heretofore, did not flower where they were exposed to the normal length of day, nor did the plants in the tests receiving 15 hours of light each day (fig. 1).

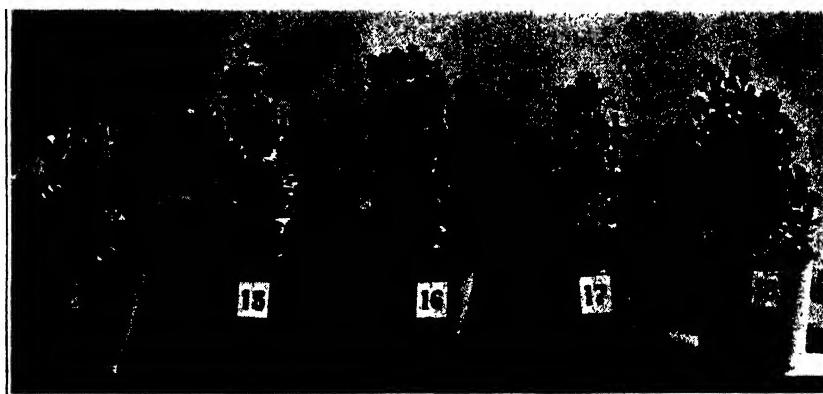


FIG. 1. The results from exposing *Sedum telephium* to various lengths of day. Controls and 15-hour plants never budded. The plants receiving 16, 17 and 18 hours illumination flowered freely.

Flowering occurred in the 16-, 17- and 18-hour tests on June 26, June 20 and June 18, respectively, at 22, 18 and 20 inches in height. Where 18 hours of daily illumination have been afforded the plants, the date of flowering has been advanced more than one week as compared with 16 hours of light. The mean length of day at Washington, D. C., from April 11 to June 21, is some-

what less than 14 hours, which appears to be considerably below the critical minimum period that will induce this sedum to flower. In southeastern Vermont, latitude 43° , where flowering takes place in summer, the mean length of day from May 21 to July 21, a period of two months, is somewhat above 15 hours from sunrise to sunset, not including effective twilight periods. It would appear that the latitude of Central New England is very near the southern limit at which this sedum can normally be expected to flower in our gardens.

The range of *Sedum telephium* in its native home appears to extend from Central Europe to Siberia, or roughly from latitude 45° far northward. Its European range agrees well with the relation between latitude and its flowering possibilities in America.

The common garden stonecrop, *Sedum spectabile*, has a much lower critical minimum length of day for initiation of flowering. In tests with constant day lengths of 14.5, 14, 13.5, 13, 12.5, 12 and 10 hours, flowering took place sparsely on the 13.5 hour day. At all higher day lengths including the control plants receiving the full day, there was profuse flowering. It would appear that a mean length of day of not less than 13.5 hours in midsummer is required by *Sedum spectabile* before it can flower. Other conditions being met, this sedum could scarcely flower at latitude 23.5° with the midsummer length of day barely reaching 13.5 hours. At lower latitudes well within the tropics flowering would cease. As a matter of fact vigorous flowering seems to require a mean midsummer day length of little less than 14 hours, a condition which would not obtain until a latitude of 28° or 29° was reached. It may be stated that in spite of the most favorable temperatures these long-day sedums become strictly dormant in the greenhouse in winter time in response to the very short lengths of day which prevail at this season.

It is evident that the stone crops, *S. telephium* and *S. spectabile*, find natural barriers to their natural distribution southward in the shortening days characteristic of lower latitudes.

Tithonia rotundifolia (Mill.) Blake, a typical short-day plant, must, from its narrow length-of-day requirements, find barriers to a more northern distribution in the lengthening days of higher latitudes. Experiments have shown that *Tithonia* does not flower at Washington, D. C., until the seasonal length of day declines to or falls below 12 hours. If these potentialities remained fixed, such plants could never extend their range far northward, since they are not only frost sensitive, but also highly specific in their requirement of short days demanded for the initiation of flowering. The requirement of a length of day of not more than 12 hours duration to induce flowering must restrict their range to regions not far from or actually below the 30° parallel of latitude, for survival depends upon the production of seed before frost ensues. There are few continental regions where frosts would not kill the plants before maturing seed in any latitude where the summer day much exceeds 12 hours in duration. It may be said that the northern distribution of

this plant is found in the Coahuila region of northern Mexico; it is not found in Texas.

The behavior of the composite *Tithonia* appears to be typical for many tropical and subtropical plants. Depending upon the narrowness of their length-of-day requirements, the longer days of extra-tropical latitudes may become an impassable barrier to a northward distribution in out-of-doors culture. A great variety of tropical plants have been grown at Washington, D. C., including Roselle, *Hibiscus sabdariffa*, tropical species of beans from Honduras and South America, species of sorghum from the equatorial regions of Africa lying between 12° to 15° north and south of the equator. All flowered readily in response to a 10-hour day, but a number including several equatorial sorghums, could not flower well when exposed to a 13-hour day (fig. 2). Naturally the full length of day was much too long for flowering.



FIG. 2. A sorghum from Togo, Africa, North Latitude 8° . Sowed June 17. The left 10-hour plant flowered August 2, height 69 inches; the middle 13-hour plant, height 41 inches, and the right control plant, height 33 inches, showed no signs of flowering when photographed August 18.

As a matter of fact growth in some instances seemed actually retarded by the long daylight exposures of the full day.

The behavior of typical long-day loving and short-day loving plants has been considered: it remains to consider a group of plants which have no restricted length-of-day requirements.

It is well known that a number of common annual weeds have successfully established themselves in far northern latitudes beyond their native habitat in the tropics. Among these are *Galinsoga parviflora* and common purslane, *Portulaca oleracea*. In spite of their strictly annual habits, and notwithstanding they are readily killed by frost, these plants have promptly made themselves at home in high northern latitudes. If these plants possessed the narrow day-length requirements characteristic of *Tithonia* and *Poinsettia*, their northward invasions would have been quite out of the question. How, then, have these tender tropical plants shown their fitness to survive as annual weeds in our northern gardens? Simply by being so generalized, nonspecific or indeterminate in their day-length requirements, as to be able to flower and fruit in midsummer from seed under all lengths of day experienced from Canada to the tropics. On the basis of its length-of-day requirements, it is this type of tropical plant alone which is potentially a cosmopolitan capable of adjusting itself to short summers far outside its tropical home.

The successful flowering and fruiting plants of our gardens coming from the tropics must obviously be plants of this potentially cosmopolitan type with respect to their day-length requirements. They must flower and fruit before autumn frosts kill them to be successful as ornamentals in our garden plantings, or to make their cultivation for fruit worth while. The tomato is of this particular type, strictly tropical originally, highly sensitive to frost, yet capable of flowering, as experimental tests have shown, in response to the longest summer days of most northern latitudes, or in response to the shortest winter days of only 8 or 9 hours duration or even less. The egg plant and pepper are plants of similar origin and behavior.

Many of our native eastern plants fall in the relatively short-day group, for flowering occurs around mid August with striking regularity year after year in the Washington region. These annual dates of flowering with some species are so regular as to excite wonderment, affording a parallel to the extremely regular arrivals of certain species of birds in their migration appearances close around the mean date of arrival.

It is a matter of common observation that many flowers are strictly autumnal in their flowering, among these being the asters, golden rods, the rag-weeds and hosts of others. In tests using a length of day of 8 or 10 hours, these short-day types can be induced to flower in midsummer weeks, months before their normal flowering time. When the daylight period is extended to 12 or 13 hours, flowering has been progressively retarded. Our earliest variety of golden rod, *Solidago juncea*, sometimes flowering in late June or early July, has been shown to be much less narrow in its daily light requirements

with respect to duration. Some of the later types of aster and golden rod, among the latter being *Solidago altissima*, are narrower in their day-length requirements, and therefore later in flowering, for they must wait until the length of day has decreased to or near 12 hours, before flowering can be initiated. This late initiation of the flowering impulse, coupled with a gradual downward trend of the temperature mean, tends to make certain autumnal plants very late.

Unquestionably the matter of retardation by lowering trends of temperature is an important factor in the autumnal flowering of certain plants. With the long-day types the factor of temperature is less specifically shown since the flowering of these plants is initiated in midsummer while the mean temperature is advancing toward the highest summer values. This relationship in which temperature and length of day are working together in the most positive manner must favor a rapid development of mature seed in strictly long-day types of plants and in indeterminate types flowering in the short summer of high latitudes.

The rapid decrease in length of day is especially favorable to successful flowering in short-day types of plants found in northern regions, since it tends to offset the lower mean temperatures naturally prevailing in summertime in such regions. This nice adjustment of seasonal factors unquestionably plays no small part in the distribution of the ragweeds, and their successful flowering and fruiting in the latitudes of lower Canada and New England. The ragweeds are so unimportant in the British Isles as to receive no mention as a British weed by Morse and Palmer in their book "British Weeds." This cannot well be explained except on the basis of their day-length requirements coupled with the fact that when the days have shortened sufficiently from their maximum length of 16.1 hours at the 50° parallel of latitude, north of which the British Isles extend, the mean temperatures are too low to promote successful flowering and fruiting before the advent of cold weather. Since the length of day is well above the critical for timely flowering, the daylight factor is not only unfavorable, but the temperatures are unfavorable. These working in conjunction to oppose early flowering would make it very difficult for any annual cold-sensitive plant with day-length requirements for flowering somewhere below 14 hours to acclimatize itself by seed production.

Tests have shown that when short-day types of plants such as certain late varieties of chrysanthemum, Klondyke cosmos, poinsettia or ragweed, *Ambrosia*, are subjected to a series of daily light exposures, the initiation of flowering remains practically constant when a certain minimum day-length value is reached. Klondyke cosmos submitted to tests beginning May 12, and grown under constant daily exposures of 10, 12, 12½, 13, 13½, 14, 14½, and 15 hours of daylight, responded as follows:

	Buds	Anthesis	Height
10-hour.....	June 3	June 18	39 in.
12-hour.....	June 4	June 18	27 in.
12½-hour.....	June 4	June 18	30 in.
13-hour.....	June 8	June 26	44 in.
13½-hour.....	June 27	July 15	45 in.
14-hour.....	Remained vegetative.		
14½-hour.....	Remained vegetative.		
15-hour (Control).....	Did not flower until the short days of October and November had been reached.		

Slightly below 13 hours the time of flowering of Klondyke cosmos in these tests has reached its lowest value. With the longer daily exposures, the time of flowering has been progressively delayed until flowering has been inhibited with daily exposures above 14 hours. There is every reason to believe that an accurate knowledge of the day-length requirements of plants considered in connection with their temperature, soil-chemistry and water-relation requirements will aid very materially in a correct interpretation of the natural ranges of plants. The behavior of the low ragweed, *Ambrosia elatior*, and the giant ragweed, *A. trifida*, when subjected to a series of day-lengths ranging from the full day in the Washington region to a constant day-length of 10 hours is of some interest. The latter, while showing nearly the same day-length requirements under certain conditions seems to hasten flowering to a greater degree than the former more especially in response to the longer day-lengths near the critical for flowering (fig. 3). Under the same conditions the giant

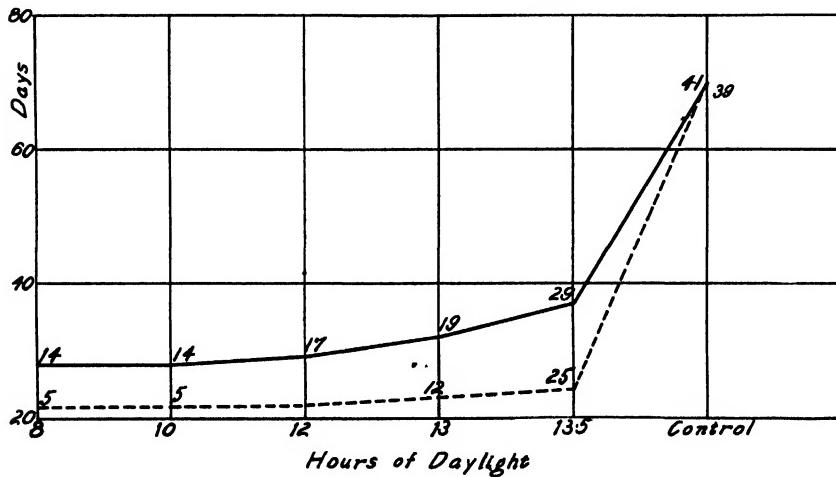


FIG. 3. Time of flowering of giant ragweed and low ragweed in response to different lengths of day. Figures on graphs represent the growth in height for each length of day when flowering took place. As longer days near the critical upper limits for flowering are approached, more time for flowering is required.

ragweed likewise appears to grow more rapidly. This behavior is reflected in the wild state, for the giant ragweed usually flowers somewhat earlier than the low ragweed, and is usually first to cease flowering. The distribution of

the giant ragweed appears also to extend somewhat farther northward, its range being well into Quebec. It is possible that this demarcation of distribution is dependent upon slightly different potentialities for flowering on a longer day-length, or it may be influenced by a capacity for more speedy flowering under certain conditions in the higher latitudes of its range.

When the flowering behavior of plants is compared under a long series of constant lengths of day, it is indicated that the ability to flower may depend upon very narrow ranges in length of day near the critical limits for flowering. Many species have been studied in normal daylight using darkhouses to exclude the light. Lengths of day differing by half hour intervals, have ranged from the full day at Washington, D. C., that is, 14 hours 54 minutes from sunrise to sunset, down to 10, 8 and even 5 hours. The behavior of the plants studied exhibits very different ranges in day length requirements of different species.

Many species appear to have a narrow critical length of day which will induce flowering. In fact a difference of one half hour may show normal stem elongation and abundant flowering on the one hand, and a low, leafy rosette condition on the other. As the length of day is increased near the critical, the time of flowering of some species is progressively retarded, and flowering may be sparse or even abnormal. A weak impulse in the direction of flower-bud formation may be shown, the buds finally being absorbed, as active vegetative expression dominates the weak flowering impulse. In other instances, the apex of the flower stem may show cessations of growth with branching which is the precursor of the racemed or panicled inflorescence.

With *Rudbeckia hirta*, flowering was normal in tests affording 14.5 hours of daylight each day. Fourteen hours of daylight, however, reduced the plants to a low, leafy rosette condition, characteristic of the late fall and winter condition.

A variety of the common garden chrysanthemum flowered in response to 12.5 hours of daylight, buds appearing June 8 and open flowers July 7. Thirteen hours of daylight induced the formation of buds June 8, but these remained dormant, firm and green until September, more than three months from the time of their visible inception. Flowering finally took place in response to the normal seasonal decline in length of day, which did not fall below 13 hours until September 1. A day length of 12.5 hours was not reached until after September 11.

Poinsettia showed no indications of flowering in response to 13 hours of daylight. Twelve and one half hours of daylight caused buds to appear July 5. The red bracts, however, had failed to develop the normal uniform deep red coloration free from admixtures of yellowish green and green two months later, whereas the plants receiving 12 hours of daylight revealed buds June 29, and the bracts were in full deep color August 3. Poinsettia plants given daily exposures of 10 hours of daylight showed buds June 22, and the bracts fully colored July 11.

While it is an easy matter to determine rather sharply defined limits for flowering in tests making use of constant daily exposures, the problem of applying such data to explain the exact times of flowering of the same plants in response to the natural seasonal length of day is not simple. The seasonal length of day is never fixed, the summer maximum occurring at the solstice. Furthermore the daily increments in spring and decrements on the autumn side vary decidedly with latitude. These factors coupled with increasing or decreasing temperature-means influence the seasonal flowering behavior of every plant. As a matter of fact, until the seasonal swing has brought the length of day well within the critical limits for flowering, where, other conditions being equal, the time of flowering has become constant, the plants are being exposed to a changing or moving mean length of day. This moving mean gradually increases or decreases toward those conditions of length of day where a constant time for the production of flowers is obtained provided temperature conditions are at their optimum. The problem of predicting exact flowering time under these conditions becomes a matter of great difficulty.

The behavior of golden glow shown in figure 4 is of interest in this connection. In these tests beginning April 12 for the controls, the 10- and 12-hour tests, the controls required 113 days to flower. The 14-, 13.5- and 13-hour tests began May 1, and the 14.5-hour tests began May 18. At Washington, D.C., these tests with the longer day-lengths were begun on these later dates, because 13.5 hours of daylight from sunrise to sunset does not begin until April 21, 14 hours of daylight not until about May 1, and 14.5 hours of daylight not until May 21. While the plants given 14.5 hours of daylight flowered in 58 days, those given 14 hours of daylight required 75 days. Although the height of the plants has been considerably reduced, rate of growth has also been greatly decreased. This retardation of flowering appears to be the normal behavior of plants when the length of day is approaching limits unfavorable for the formation of flower primordia. Golden glow, a plant with long-day requirements, finds this limit on a decreasing length of day lying between 14 hours and 13.5 hours, which is near the lower limits for flowering. In the case of Peking and Biloxi soybeans, poinsettia and the ragweeds, it occurs on an increasing length of day approaching the upper limits of flowering. Since golden glow shows conspicuous stem elongation in response to 13.5 hours of daylight, it is possible that the plants ultimately would have flowered if these conditions of length of day had been long prolonged. However, when the natural seasonal decline had brought the day-length to 13.5 hours August 21, there were still no indications of flowering. The long time, 113 days, which the controls have required to flower, must be explained in part as a response not only to the lower mean temperatures in April and May, but also to lengths of day which at the beginning of the test were below limits favorable to prompt flowering. Although the tests began April 12, the mean length of day until May 15 was only 13.5 hours, which, as the photograph shows, pro-

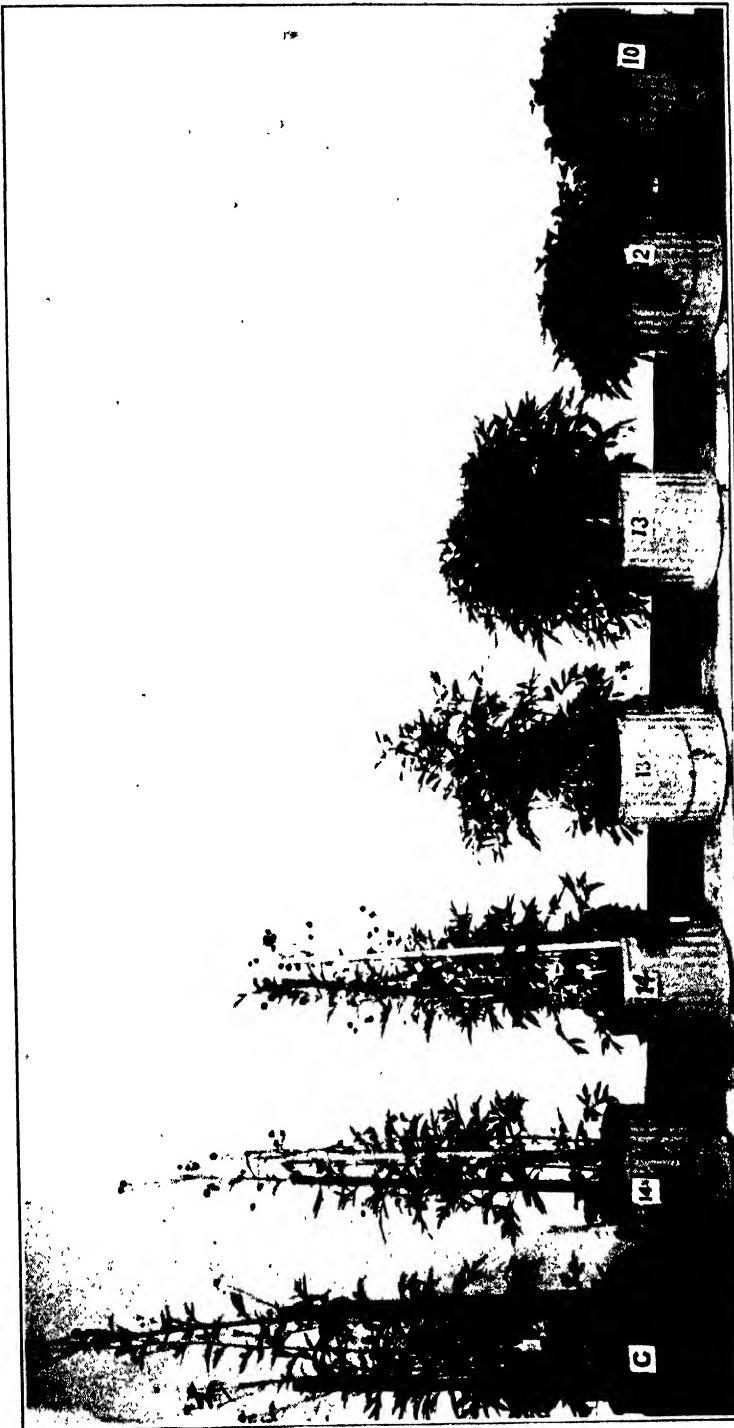


FIG. 4. The golden glow, *Rudbeckia laciniata* L., showing response to different lengths of day. Flowering occurred in all plants exposed to a day of 14 hours or more. There was only leaf rosettes with 10- and 12-hour days, some stem elongation with the 13-hour day and more with the 13.5-hour day.

motes stem elongation alone without flowering, at least for a long period of time. A length of day of 14 hours, favorable to flowering even though delayed, does not come into actual operation until about May 5.

Since days of 13.5 hours do not promote prompt flowering, it can be assumed that the period prior to May 5, that is, 24 days, had little to do with the initiation of flowering. This number of days deducted from 112 days required by the controls to flower leaves 88 days actually long enough to be associated with preparation for flowering. If a constant 14-hour day had operated during the entire period from May 5, when 14 hours of daylight begins, until flowering was initiated August 3, 90 days would have elapsed. As a matter of fact, 14.5-hour days begin May 21 and continue at or above this value until July 21, a period of 61 days. The requirement of 58 days to flower which occurred in response to a constant day of 14.5 hours would, counting from May 21, place the time of flowering near July 18, whereas the actual date of flowering was August 3, this date marking the seasonal termination of a length of day of 14 hours. There would seem to be discrepancies here not readily explained on the basis of length-of-day responses. However, a critical analysis must take account of the following facts and relations which are associated with flowering in response to the changing seasonal length of day. Discounting all days shorter than 14 hours, which tests have shown definitely to initiate flowering, the following seasonal day-length relations are found to operate. May 5 to May 21, embracing a period of 16 days with the length of day increasing from 14 to 14.5 hours, initiated flowering. Under these conditions of varying day length flowers appeared in 75 days, whereas 58 days were required in response to a fixed length of day of 14.5 hours. May 21 to July 21, embracing a period of 61 days with the length of day 14.5 hours or over, caused flowers to appear in 58 days or less. July 21 to August 5, covering a period of 15 days with the length of day decreasing from 14.5 to 14 hours, according to our data obtained from tests with fixed lengths of day, should tend to cause flowering beginning with a minimum time of 58 days increasing to 75 days. Since it is probable that the lower limits of the flowering response lie somewhere between the day-lengths 14 and 13.5 hours, with still greater retardations of flowering, it is quite possible that the complex operations of these changing day-length conditions account for the period of 88 days which appears to be concerned with the flowering of the controls delayed until around August 3. Whatever the true interpretation, it is evident that the seasonal variation must impose upon the controls a rather weird moving average of day-lengths operating around the optimum for flowering, each tending to express itself in flowering or non-flowering stages.

On the spring side of the summer solstice, strictly non-flowering lengths of day advance to lengths of day promoting flowering but with maximum retardations. As more favorable day lengths follow, these retardations decrease to some minimum time requirement of the plants for flowering when the length of day has reached optimal values. After the summer solstice, there is again

an increase in the number of days for flowering until maximum values are again attained near the lower limits favorable to the initiation of flowers. These progressions to and from the optimum length-of-day conditions for flowering together with the operation of more or less favorable temperature means, cannot but make the interpretation of the theoretical or actual range of plants on the basis of their responses to fixed lengths of day under control conditions exceedingly difficult.

Although one may determine the behaviors of plants to fixed lengths of day, it is obvious that a wild plant with length-of-day responses similar to golden glow, must limit its southward extension long before extremes unfavorable to flowering have been reached. This is true because near these limits, there may be such great retardations of flowering, as to allow low temperatures and frost to have entire control of the situation. Other conditions being equal, the more rapid increments and decrements attending seasonal changes in length of day in northern latitudes should tend more sharply to delimit flowering in certain long-day types of plants, than in the lower limits of their range. The factor of lower mean temperatures in northern regions is one of great importance in the final behaviors of organisms, applying both to insects and to plants. In spite of these complexities, however, our data secured under constant lengths of day must be of some service in an understanding of the range and seasonal flowering of many plants.

With respect to the length-of-day requirements of plants, it cannot be dogmatically stated by mere inspection of the floral facies of a region what the day-length limitations of a given plant may be. On a strictly length-of-day basis, however, plants with long-day requirements whose flowering and fruiting is rigidly restricted to the very long days of high latitudes such as *Sedum telephium*, would naturally be excluded from tropical subtropical and even the warmer temperate regions of the earth. The natural extension or the artificial extension by man of the range of these plants, must follow belts or zones more or less parallel to the equator. It is likewise obvious that frost-sensitive plants with greatly restricted requirements for short days of 12 hours or less, must confine themselves within the tropics. Their zonal distribution must normally follow easterly-westerly lines in the warmer regions of the earth where the days are relatively short.

Indeterminate plants, alone, are potentially world-wide wanderers, since they have no narrow day-length restrictions imposed upon them. It is in this class of plants, common both to high and to low latitudes, that one may expect to find material suitable for widespread introduction northward or southward. The indispensable tomato of the tropics is an outstanding example of this class.

In the normal migrations of plants, unquestionably the forces of life have had to make infinite adjustments to this factor of length of day throughout the world, quite as rigidly as to temperatures, soil moisture and other conditions. It is evident that in the final permanent adjustments, the regional

floras must take on a physiological facies comparable to that which has finally obtained in arid or humid regions, and in regions of heat and cold. In the case of soil moisture, this has extended to a very distinctive morphological facies, with the xeric or arid region forms at one end and the mesic or hydric forms at the other. With respect to the length-of-day factor, this adaptation must have been a problem quite as profound for the plant. While peculiar and distinctive vegetative structures have not been demanded of the plants, synchronisms of flowering with the most favorable lengths of day for the warm growing season had to be met with much nicety in countless ways. The result seems to be that the equatorial plants in the main must be either indeterminate in their flowering or of the typical short-day behavior. The typical long-day types would acclimatize themselves successfully in the more northern latitudes alone. The indeterminate and certain short-day types whose upper limits for flowering are not too narrow alone possess physiological potentialities for adaptation in both tropical and in northern latitudes, other conditions being equal.

A proper recognition of the length-of-day requirements of plants makes possible a clearer interpretation of many aspects of their behavior and natural distribution than we have had heretofore. In our artificial introductions, this factor must be taken into account, especially where flowering and fruiting appears to be disturbed. The entire matter may depend upon maladjustments in this direction which have been overlooked. Once this is shown to be the factor, changing the daylight durations intelligently toward longer or shorter periods may be quite within one's power oftentimes. It is unquestionably true that man for ages has unconsciously selected for better seasonal adjustments, and in these activities all his early and late varieties for northern or southern regions reflect in greater or less degree relationships with the ubiquitous length-of-day factor in one way or another. Until strains are found with much wider day-length requirements, many promising tropical plants must be confined to the tropics, however useful they may be. Careful studies of large populations, however, may reveal variations in the direction of strains flowering and fruiting under longer days.

A study of the behavior of many plants at Washington, D. C., in response to a series of lengths of day ranging from 15 hours to 10 hours, decreasing by half-hour intervals, has been of some interest. The greatest individual variability in the date of first flowering is shown near the critical limits for flowering. Well below the critical length of day favorable for flowering, the close synchronisms of flowering become striking. This behavior would suggest that attempts to secure strains or races of plants suitable for other latitudes should be based upon selection made near the critical length of day for successful flowering and fruiting. Tests with many plants have shown that marked individual differences of behavior come into expression here where none is shown in response to day-lengths well below the critical that will initiate flowering.

LIFE ZONES AT MOUNT RORAIMA

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The object of the following remarks is to present as complete a picture as possible of the general ecological aspects of the territory in the vicinity of Mount Roraima from data gathered during a few months visit.

Since the topography of the area has been dealt with in some detail in another paper (Tate, '30), only a few cursory remarks in that respect are now necessary. Mount Roraima, standing at the junction of the three states, Brazil, Venezuela and British Guiana, is the largest of a group of table mountains derived from identical sandstone and igneous formations. Completely encircled by sheer cliffs twelve hundred feet in height, this imposing block of sandstone reaches an altitude of 8600 feet above sea-level. The area of its rough but approximately level summit, which is almost entirely devoid of soil and vegetation, is some twenty-five square miles. The remnants of a volcanic sill, whose slopes reach outwards and downwards for from five to ten miles, support the sandstone beds of the upper, precipitous part of the mass. On the northeastern side the slopes merge with the forests of the Mazaruni drainage, and to the southwest with "upland savannas."

Vegetation is rather markedly divisible into groups which frequent summit, slopes and savannas, the distinctions being accentuated by temperature and rain-fall contrasts. The chief environmental divisions and the major factors governing them are shown as follows in order of altitude:

Laterite savannas and forests.—The country rock is chiefly composed of iron laterites, the end-product of weathering of diabase. The climate is sub-tropical to tropical (6 a.m. temperature average 64°), with well-marked wet and dry seasons, the latter showery during afternoons. The altitude is from 4000 feet (Paulo and Arabupu) to 4500 feet.

Diabase slopes.—The country rock is chiefly diabase, but includes a local sandstone exposure and scattered sandstone talus. The climate is sub-tropical (6 a.m. temperature average 59° at Rondon Camp and 61° at Philipp Camp), with intense to moderate rain-fall. The altitude at Rondon Camp is 6900 feet, and at Philipp Camp is 5200 feet (the top of the talus slope at the foot of the cliffs is 7400 feet).

Plateau.—The country rock is sandstone, mainly without soil. The climate is sub-tropical (morning temperature average 52°), with intense rainfall. The altitude is 8600 feet.

The first two zones provide wide ranges of climatic variation which result in a number of sub-regions, often conditioned by exposure, which are dealt with in the course of the paper.

The dry season with its occasional afternoon shower lasts from October to March, and usually reaches its maximum in January. Except during unusual years of intense and prolonged drought, when the mountains may remain clear for weeks together, a cloud-belt maintains itself about the upper slopes and cliff-faces and causes the intense humidity of those parts. During each summer local Indians—Partamonas and Arecunas—are accustomed to burn off the grass-lands. In very dry weather the fires enter the forests and destroy or greatly alter them. Most of the characteristic plants are wiped out, and replacement forms spring up in their stead. Even in patches of woods which appear little damaged, examination shows more than fifty per cent of the trees dead. The remainder have their lower parts buried beneath dense layers of bracken and festoons of razor-grass. Walking in such a tangle is next to impossible; moreover, animals and birds, whether due to extinction by fire or to the present unfavorable conditions, are almost absent. In April, 1926, at the end of one such unusual season, fire destroyed most of the woods that grew upon the southern and eastern flanks of Roraima and its sister mountain, Cuquenam. (A traveler, Mr. D. Holdridge, has since stated that his porters started the fire on April 3d during his ascent of the slopes and has shown us a photograph of the fire.) The blaze even reached the plateau by way of the "ledge" or inclined rocky shelf leading to the summit, but made no progress among the scanty vegetation there. Notwithstanding the general destruction, at various altitudes on the slopes below the sandstone cliffs sufficient patches of forest survived for us to assemble representative collections.

The following five collecting stations, four of them on the southwest slope, were chosen in places from which every type of environment would be readily accessible: Arabupu, 4000 feet; Paulo, 4000 feet; Philipp Camp, 5200 feet; Rondon Camp, 6900 feet; Summit Camp, 8600 feet. Arabupu and Paulo are complementary. The first, rather biologically unproductive because of the recent fire, served as a base for the trail to the summit. The second, southeast of Roraima, was chosen because there the vegetation was less injured. Both Arabupu and Paulo are small native villages and the other stations merely camp sites.

PAULO AND ARABUPU, 4000 FEET

Paulo, an Arecuna village some seven miles to the southwest of the cliffs of Roraima, stands at the tip of a ridge springing from the Cuquenam foot-hills. The Cuquenam River and another stream to the west, which unite a quarter of a mile farther south, flank the ridge.

From the crest of the ridge at Paulo with his back turned to Roraima, one looks out over a vast expanse of grasslands rising and falling over endless series of smoothly dissected ridges and valleys. Here and there, particularly in re-entrants and along watercourses, the green savanna is interrupted by

isolated patches of tropical forest; or occasionally, small areas of brushy growth may be descried nestling in depressions in the ridges. Now, facing the mountains, one looks out over the Cuquenam valley onto the ever-rising, billowy foothills that sweep grandly up to the base of Roraima's bare red cliffs. To the naturalist the sight of the thousands of dead trees still standing on these slopes is a tragic one. Here, but a few years ago, this great forest, with occasional fingers of grassland running far up into it, formed one of the richest, most diversified, and least explored plant aggregates in South America. All that remains of it is a few scattered remnants dotting the gullies and along the base of the cliffs. At Arabupu conditions are not so bad and much splendid aboriginal forest remains. The line separating forest and savanna is startlingly abrupt, and seems to wander along at random. Here a savanna embayment forms a retired and picturesque meadow. There a patch of woods stands alone in the prairie or joined by a narrow tongue of trees to the main forest.

Before the conflagration the forest on the Cuquenam and Roraima slopes extended to within half a mile of Paulo; now, excepting a few small portions, damaged but not wholly destroyed, its place is taken by a deep mat of bracken, with innumerable bare, whitening tree-trunks thrusting through. Pokeweed, usually mixed with the all-pervading bracken, has appeared very abundantly as a replacement plant at altitudes of 4000 to 6000 feet.

The steeply sloping, dissected country south and east of Paulo is for the most part devoid of forest. Indeed, over much of its extent the land appears never to have been forested; and small pockets of forest, invariably much damaged by fire exist only in sheltered ravines and re-entrants. The character of these small tracts is similar to that of the extensive woods at Arabupu. The laterite savannas, due partly to the poverty of the soil and partly to repeated burning, exhibit a decided paucity of fauna and flora; so, of necessity, plants which maintain themselves there are equipped with rhizomes and roots resistant to drought. On the Paulo ridges the plants may be tough shrubby growths or slender resilient grass-like forms; leaves are shining coriaceous, or hairy (light-diffusing and moisture-retaining). On the slope between Paulo and Philipp Camp at 4500 feet (and apparently nowhere else) grows a straggling mimosaceous bush dotted with great heads of beautiful crimson stamens. Its flowering season is over by the end of October.

The Cuquenam River along most of its course has cut down for eight or ten feet into "jasper," the green rock underlying the diabase sill, which is exposed only in river-beds. Its walls bear a cliff flora of shrubs, *Drosera*, *Bromelia*, ferns and Lentibulariaceae. Up-stream, sedges, bladderworts, and other plants grow on small deposits of silt and beyond an old flood-plain supports a tangled mass of grasses, bracken, *Lantana* and *Hyptis* four or five feet in depth.

Further remarks upon the upland savanna country are based on the similar station at Arabupu, nine or ten miles to the east of Paulo.

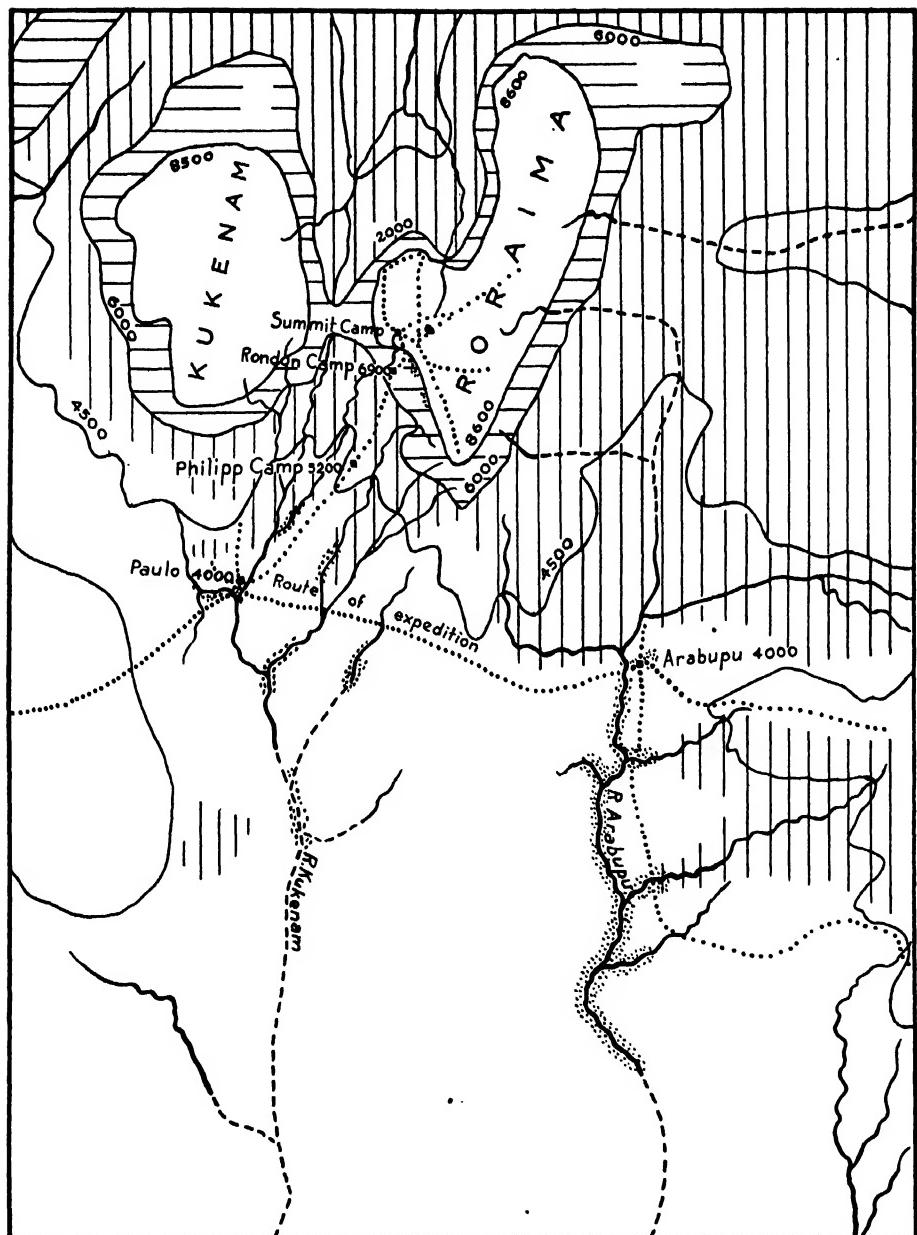


FIG. 1. The Mt. Koraima District. Route of the Lee Garnett Day Expedition is shown by dotted line; the finely dotted areas are river-fringe forest; the open areas are savannas; the lined areas are forests. Heights are given in feet.

The village of Arabupu, with a population of about fifty Arecunas, is named after the river on whose bank it stands. The river (Arapape on Brazilian maps) begins as a thin, silvery cascade falling from the cliffs of Roraima near the middle of the southeast wall, and joins the Cuquenam River some twenty-five miles to the south. Its valley is broad, chiefly savanna-covered, bordered on either hand by rolling hills from which issue numerous tributary streams. A mile or so to the north of the village the grass-lands terminate. The border of the great forest of Weitipu, stretching unbroken for some ten miles to the northern slopes of the mountain of the same name, lies half an hour's walk to the southeast. Even here fire has consumed parts of the woods. As at Paulo, wherever this has happened that portion is rendered impenetrable for collectors by matted growths of razor-grass. The forest of the upper slopes of Roraima on the Arabupu side seems to have been spared even less than at Paulo. Except at the northern end of the slope no green is visible above 5000 feet.

The soil is predominantly laterite; but the river-bed is cut down to the jasper (Tate, '30, p. 60), in which, near the village, a waterfall thirty feet in height has been carved. Above the falls the water flows over exposures of jasper only in a few places; elsewhere its course is over large, rounded stones of quartzite coated with yellowish, iron-stained silica. Climate at Arabupu is similar to that at Paulo, but work was done there in January, the driest time of the year, instead of in November.

Arabupu includes several types of habitat—forest, savanna, small swamps, river and brook-side.

As will be seen from the sketch-map (fig. 1), the extensive forests of Arabupu, starting from the southeastern foot-hills of Roraima curve around the northern end of the valley and over the ridge reaching southeast to Weitipu, and connect with the forest of Weitipu (figs. 3, 4) at its northern edge. In addition, small patches border the tributary streams of the Arabupu. Forest grows chiefly on the hill-sides; the ridge-tops and river-valleys, except for strips of gallery-woods in the latter (fig. 5), are mainly savanna-clothed.

The forest contains many species of large trees of striking appearance. An especially prominent one, crowned with masses of deep yellow flowers, appears in the woods only occasionally. It has proved to be a new species of *Ouratea* (Ochnaceae). Specimens were collected at the end of December. Trees possibly allied to this species were seen in flower in October in the forests southwest of Cuquenam. Undergrowth, which is comparatively thin and easy to pass through, has very few plants in flower at this season.

Gallery-woods bordering the river and streams contain several characteristic woody forms. In October at Paulo a small tree (*Simarouba*?), prominent on account of bunches of purple flowers, is a feature in the fringe of woods along the Cuquenam.

After emerging from the forest near Roraima the Arabupu flows through savannas and has few bordering trees until it has passed below the falls.

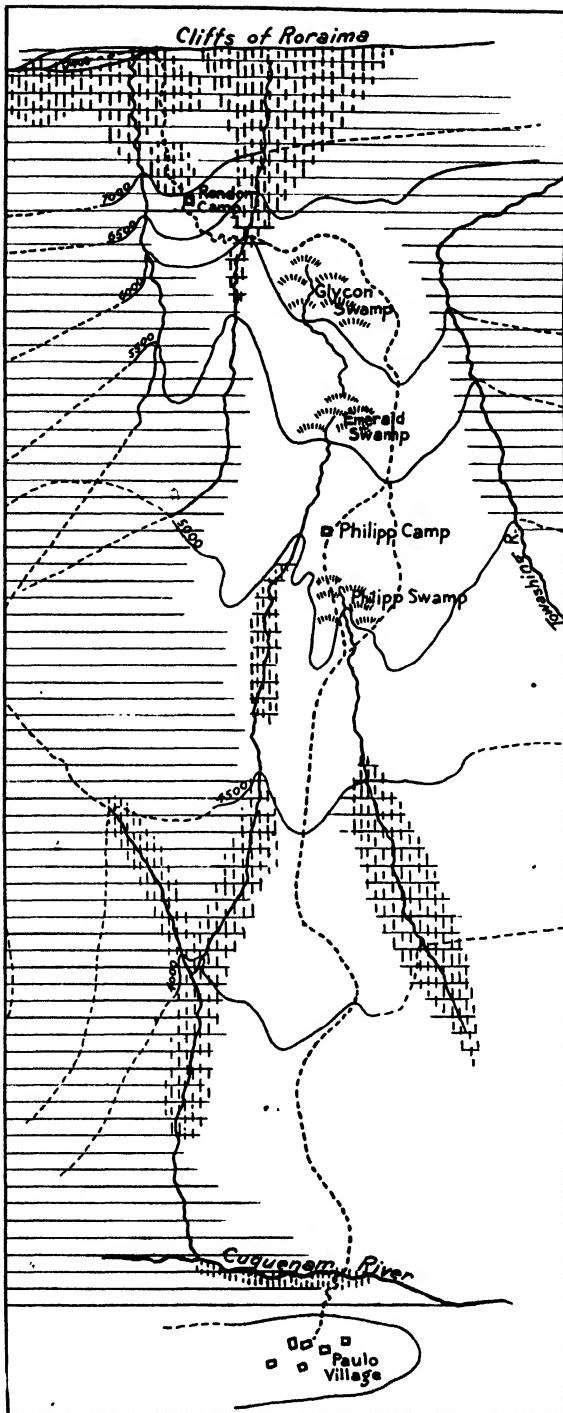


FIG. 2. Diagram of the slope from Paulo village to the base of the Roraima cliffs. White areas are savannas; horizontally lined areas are original forests before the fire; vertical broken lines are existing forests.

There it becomes fringed by bank-forest. Above the water-fall its bed is stony, farther down rather muddy; but the water remains clear, being only discolored slightly by the humus of the forest in which it originated. Along the edge of the stream the bushy tree, *Mahurea exstipulata*, is particularly noticeable in December because of its large clusters of dull, cherry-pink blossoms.

The grass-lands fall into two poorly defined groups: the open ridge-top and slope; and the predominantly flat prairies along the bottom of the Arabupu valley. Both sorts are found also at Paulo, but certain plants not noted at Paulo are observable at Arabupu. In certain places the ridge-tops are partly covered with bushy *Cyrilla brevifolia* and *Clidemia rubra*. Again, in gently-

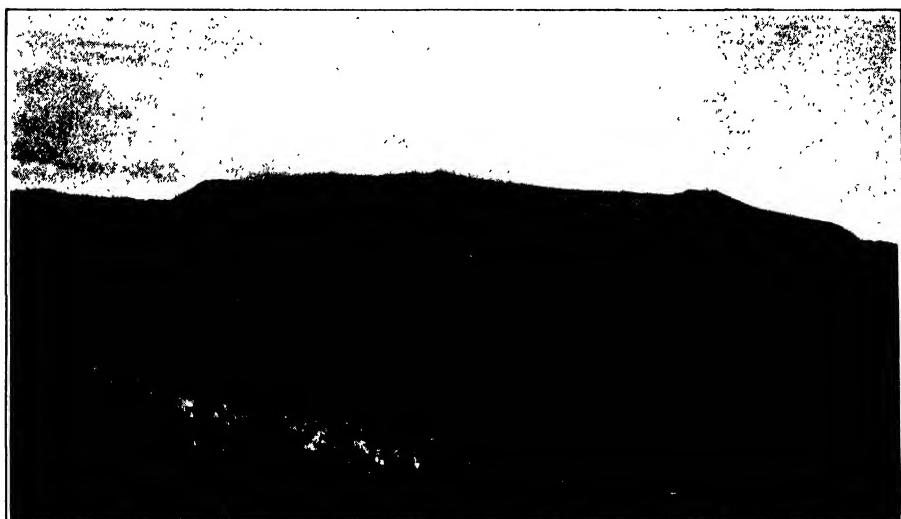


FIG. 3. Mt. Weitipu seen across the Weitipu forest (4000 ft.) from near Arabupu.

sloping meadow-like portions forming the transition from hill-side to the valley prairies milkwort, *Polygala hygrophila*, yellow-eyed grass, *Sisyrinchium alatum*, and tiny white-flowered gentians, *Curtia tenuifolia*, occur. At the extreme northern end of the savannas (fig. 6) in meadows nearly surrounded by forest seemingly local plants, *Croton subincanus*, *Ichthyothere cunabi*, *Baccharis* sp., and *Tibouchina aspera* grow.

A short way above the water-fall on the left bank two very swampy depressions in the flat-lying savanna exist. That farther depression produces the Bromeliad (*Brocchinia reducta*), as its dominant plant-form, but contains also a sprinkling of the diverse flora of the nearer.

Whether due in some way to the prevailing laterite, diabase, and quartzite, or only to fire and hunting by Indians, most forms of mammals are comparatively scarce, not only on the summit and higher slopes of Roraima, but over

the extensive territory at its base. The forest-inhabiting kinds are all rare and without traps almost none can be secured. Even the Arecuna hunters on their forays have trouble to find the deer and tapir they seek. It is true that from twenty to thirty small animals were caught by us each day, but only because a line of nearly five hundred traps was maintained.



FIG. 4. A brook in the interior of the Weitipu forest.

In addition to true forest forms, a few live more or less associated with and restricted to the rivers, particularly the Arabupu. The water-rat (*Nectomys*) and the capybara are truly aquatic in habit, and two species of spiny-rats (*Proechimys*) habituate the wooded river-banks, where their footprints can commonly be seen in the mud.

Characteristic savanna mammals are the partly diurnal grooved-toothed cotton-rat (*Sigmodonmys*), field-mouse (*Zygodontomys*), and giant ant-eater



FIG. 5. Gallery forest along the Arabupu River through which fire has passed.
Note the bracken fern replacement.



FIG. 6. The extreme northern end of the savannas at Arabupu. Mt. Roraima is at the left in the distance and Mt. Weiassipu is in the center distance.

(*Myrmecophaga jubata*). The small animals are plentiful locally, especially where the ground is broken up or where there are many old termite nests. Tracks of gray-fox (*Urocyon*) were seen only once at Arabupu. These animals, although frequently met in the lowland savannas, do not seem at all common near the Roraima foothills.

Bats were not plentiful. At Paulo specimens of *Molossus* were brought in, probably secured in some cave. A specimen of *Artibeus* was also brought to the skinning table. Rarely, *Myotis* or *Eptesicus* were seen flying at dusk.

In the Arabupu swamps no mammals, few birds, and no reptiles or amphibia were observed.

Birds of the Arabupu forests comprise many species, chiefly ant-birds, woodhewers, mannikins, warblers, vireos, tanagers, cotingas and hummingbirds. Certain kinds, definitely associated with the river or its fringing forest, include finfeet, kingfishers, rough-winged swallows, and perching types like swallow-winged puff-birds, jacamars, and various tyrants of the genera *Megarhynchus*, *Myiobius*, *Myiarchus* and *Elacnia*. The gallery woods in the early morning are the favorite resort also of *Amazona* parrots, parakeets of the genus *Conurus*, and stealthy tiannamous. Savanna birds, as is usually the case, although individually plentiful, are relatively few in species.

Besides coral and tree snakes, the fer-de-lance (*Bothrops atrox*) is not uncommon in the forest, especially at the edges on sunny afternoons; while among the trees the little lizard (*Anolis nitens*) abounds. The South American rattlesnake (*Crotalus terrificus*) is dangerously common on the savannas. In addition, two or three harmless varieties of snakes are found. Innumerable sun-loving lizards of the species *Ameiva praesignis* and *Tropidurus hispidus* scamper with swift, jerky movements through the grass. The toad (*Bufo granulosus*) is plentiful at Paulo in small water-filled holes on the ridge near the houses.

A small collection of fishes, most of which are from the Arabupu or from tributaries of the Cuquenam, has been identified. Some were killed with fish-poison, others taken with hook and line.

Grasshoppers, termites, and grass-cutting ants are noteworthy among the invertebrates. Many species of the first occur, one of which is gregarious and gathers in flocks on the ridges during October and November. All take flight at the same time when startled. Their silvery, transparent wings flashing in the sunlight remind one somehow of the glistening fins of schools of little flying-fish in the Caribbean Sea. The Indians catch and eat them, either fresh or dried and ground up. Local termites form their nests quite differently from those of the Rio Branco savannas. Instead of great, pagoda-shaped structures six or eight feet in height, they build only low, flat domes (fig. 7) some five feet in diameter and two or less in height. In addition to the leaf-cutting ants of the forests, a grass-cutting species lives in the open savanna which makes extensive, scrupulously clean roadways extending considerable distances from the nest.

Blackflies (*Simuliidae*) are particularly troublesome in this region of water-falls and fast running brooks. The persistent attack of the tiny pests makes bathing anything but the pleasure it would otherwise be. Their flight is so powerful, and they are so adept at approaching up-wind that even on breezy days they bite. Another troublesome fly, a drosophilid, is called sweat-fly. It does not bite, but it settles and crawls and tickles, and in this way becomes almost as great a nuisance as the black-flies. It appears especially numerous in newly burned areas. Near Roraima mosquitos are generally not

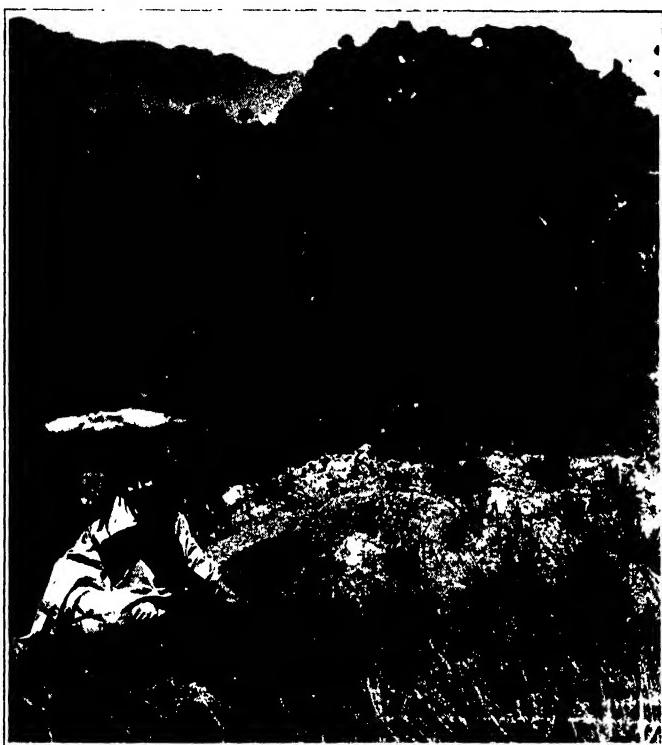


FIG. 7. A Partamona girl digging termites to eat from a typical, low, flat-topped mound.

very plentiful; but *Anopheles* is present and some of the Indians have malaria. At Paulo in November a brood of Culicid mosquitos hatched out that caused us much discomfort at night. Probably they bred in the mud-holes from which the clay for house-walls had been dug.

In conclusion, the two principal associations of the Paulo-Arabupu area are (1) forest and (2) savanna. The undamaged forest of the lower slopes of Roraima is quiet, dark and humid, without obvious signs of animal life beyond the occasional ringing call of the bell-bird, and near streams a deep, barking note of some kind of frog.

The intense sunlight, compacted clayey soil, and the specialized fauna of the open lands contrast markedly with conditions in the woods. In that environment of heat by day and chilly breezes after sun-down, the termite nest seems to form the outstanding ecological centre. Mounds spaced out some twenty feet apart can often be seen covering many acres of land. Rats, rattlesnakes, lizards, toads, even birds find shelter or food or both in them; and ant-eaters tear them apart in search of the nourishment afforded by teeming multitudes of insects.

PHILIPP CAMP, 5200 FEET

Directly up the southwest slope of Roraima and some five or six miles from Paulo, Philipp Camp, 5200 feet, is located in a little sandy plain cupped in a hollow of the hills. A stream of clear water flows not fifty feet from the camp site and joins the Cuquenam River. Numerous great sandstone boulders whose tops support certain rock-inhabiting plants, are strewn about.

In the Philipp Camp zone four distinct types of habitat, depending upon their relation to water and the water-table, are present. These, while they grade into each other at their edges, are widely different at their highest development. They are arranged in order of the water-table level: swamps; banks of the Philipp Brook; nearly level, well-drained savanna; ridge-slopes and crests.

Philipp Camp zone is limited somewhat abruptly at its upper edge by sub-tropical forest, 6000 feet. The 6000-line is strongly marked here only through the upper margin of the strip of savanna which runs up from the Paulo savanna zone. This is the only tongue of grassland of its kind, for elsewhere the slope is entirely covered with forest or the remains of forest. In the woods no sharp transition can be discovered, the lowland plants gradually giving place to vegetation of the higher zone. Such is also the case on the Arabupu side of the mountain.

Between Philipp Camp and Paulo there is no sharp line. The soil of the grassy slope is sandy in places. In others it is composed of laterite. Transition from one zone to the next is barely noticeable, and indicated mainly by gradual changes of temperature, rainfall, and vegetation.

Before it was burned, the Pinnacle ridge, across the Towashing stream, which originates near Towashing Pinnacle (figs. 1, 2) without doubt carried fine, tall forest; but now it is clothed only with tree-stumps and replacement plants. The forest that adjoined Philipp Camp (fig. 8) some years ago is also practically destroyed, and forest-inhabiting forms no longer exist nearby. Consequently any specimens of typically forest birds labeled "Philipp Camp" must have been captured either in the sub-tropical Rondon Camp zone or below in the Paulo section. That this actually took place there is no doubt, for Indians brought in birds from spots remote from the collecting station. To express the conditions of the slope from Paulo up to the cliffs, a drawing

showing the positions of various areas is included (fig. 2). The sub-zones of the slope are perhaps best spoken of in terms of soil and vegetation.

The term Philipp Camp refers also to the high savanna area at 5200 feet with porous, sandy soil. Numerous sandstone boulders (fig. 9) from the quartzite cliffs bearing indigenous plants are scattered over it. The ground varies from dry to moist, and characteristic vegetation includes grasses, sedges, *Polygala* and *Habenaria*.

Philipp Brook flows from Emerald Swamp to the lowlands. Its bed is only some six feet in width, quite steep, and full of boulders. Its flora com-



FIG. 8. Philipp Camp (5200 ft.) with Philipp Brook in the left foreground. The "ledge" leading to the summit of the cliffs is to the left. The dark areas at the base of the cliffs are surviving patches of cloud-forest.

prises lush grasses, *Hypnum*, water-mosses, and scattered trees—invaders from the old Paulo forest.

Philipp Ridge and similar adjoining ridges are formed of diabase covered by thin soils of laterite earth and a little sand. Floristically, they may be considered equivalent to the upper parts of the ridge at Paulo, and are distinguished from the Camp area only by the disappearance of certain plants. Grasses are dominant on them.

The neighboring chain of swamps, collectively named by Schomburgk "El Dorado Swamp," is here divided into Philipp Swamp, 5100 feet, Emerald Swamp, 5700 feet, and Glycon Swamp, 6100 feet—all three with considerable humic matter mixed with the sand. These sub-divisions have been based

upon differences of altitude and variations in the character of the vegetation. The names serve also to emphasize the finer environmental *nuances* expressing changes of soil, altitude, temperature and rainfall.

Philipp Swamp, 5100 feet, is filled chiefly with tall three-foot grasses, but contains numerous other plants, including *Abolboda*, *Eriocaulon*, and several Lentibulariaceae. On sunny afternoons it is the scene of much insect activity. Small hover-flies, click-beetles, and slow-flying tortoise-beetles, certain Syn-



FIG. 9. A sandstone boulder at Philipp Camp clothed with specialized plants.

tomid moths and "golden-eyes" of lazy flight, and quite numerous black-flies are encountered.

Emerald Swamp, 5700 feet, clothed almost entirely by a close carpet of mosses, chiefly *Polytrichum*, and scantily *Furnaria*, presents a vista of brilliant green, merging into coppery shades wherever the *Polytrichum* is in fruit. The swamp is approximately located between the upper and lower sills of diabase about level with the top of the lower sandstone scarp (Tate, '30, p. 61), which possibly accounts for its markedly distinct vegetation.

Glycon Swamp, 6100 feet, is partly dominated by *Brocchinia reducta* and partly by an assortment of linear-leaved plants like sedges, Xyridaceae and Eriocaulaceae. At its upper edge, before the commencement of the cloud-forest, is a belt of well-drained rocky ground on which grow several kinds of Compositae,—*Eupatorium*, *Vernonia* and *Achyrocline*. Except for the absence of the long grass, it is quite like Philipp Swamp in certain particulars. However it is more exposed nearer to the cliffs and receives more rain.

Large Bromeliads (*Brocchinia reducta*) grow abundantly both in Philipp and Glycon Swamps. Their leaf-bases are always full of water, and their leaves remain tightly rolled in tubes long after attaining full growth. Numbers of insects, even of large size, fall into these traps and their bodies rapidly go to pieces. Perhaps the fluid at the bottom of the leaf-tube contains digestive ferments and the plant obtains a part of its food from the insects, as is the case with pitcher-plants.

Traps for mammals in the Philipp Camp zone gave a poor yield. Small lesser rice-rats of the genus *Oligoryzomys* were caught occasionally, both in the lush growth of the swamps and among the mosses at the edge of Emerald Swamp. They were also not uncommon among the bushes along the Towash-ing stream on the opposite side of Philipp Ridge, and one was taken on the top of one of the great boulders. They did not occur at the next higher camp in the sub-tropical forest, and appear to go no higher than the tongue of savanna. Several of the females were with embryos or were nursing young (November). Field mice (*Zygodontomys*) closely allied to *Akodon*, were about as common, but seemed more strictly local. At Philipp Camp they were only trapped in and about Philipp Swamp, or along the Brook. Only one female was taken with young. An opossum of the genus *Didelphis* was not rare. It has the strong black and white markings of the mountain forms of the Andes, and lacks the powerful, unpleasant odor of the lowland ones. Immatures about one-third grown, as well as an adult, were captured. The name given it by the Arecuna Indians is "awari." Red howling-monkeys were reported abundant throughout the forests before the fire, but during the entire visit not a trace was seen nor a single "howl" was heard.

Rather few varieties of birds occur. Indians brought in quantities of specimens which almost unquestionably were shot in the woods of the cloud-belt and not in the savannas. The few indigenous forms are plentiful; finches, sparrows, Synallaxidae, hummingbirds, nighthawks, swifts, a mockingbird, *Pseudagelaius* (whose sharp, inflected whistle was heard in the afternoons), a meadowlark and a swallow make up the avifauna. Sparrows and finches are the most plentiful of these, but none of them is rare. Reptiles are not an abundant group as high up the slopes as Philipp Camp. No snakes were seen, and the only really common lizard is *Tropidurus hispidus*. This animal is plentiful about the scattered rocks, and its nearly black color matches the dark diabase and discolored sandstone very closely. One specimen of the

green-headed *Ameiva praesignis* was seen and at the very top of the Philipp area, quite near the Rondon woods, an *Anolis nitens* was taken.

About seventy different sorts of insects, spiders, etc., were collected. Rather common among them were the butterflies *Pyrameis* and *Junonia nigralis* (recently described by Forbes from Kaieteur), several sorts of grass-hoppers, two species of Syntomid moths, and a spider which spins a radiant web plus strands supporting an inverted, conical nest made of silk and the bodies of victims. Although the grass was full of ticks, they seldom attacked men.

RONDON CAMP, 6900 FEET

From the uppermost swamp (*Glycon*, 6100 feet), the trail crosses a brook and climbs another 900 feet through a zone of burned woods. No level ground exists on these broken slopes. A large patch of uninjured cloud-forest at 7000 feet (fig. 10) furnished the greater part of the collection from



FIG. 10. The interior of a pocket of surviving cloud-forest near Rondon Camp (7000 ft.).

the region, and from Rondon Camp it was also possible to work the remaining 500 feet up to the base of the cliffs. These forests contain many of the endemic species of fauna and flora for which the slopes of Mount Roraima are noted. The amount of rain which falls daily, only half a mile from the cliffs, is very great, and owing to the manner in which mist persistently mantles the precipices and slopes near their base, the humidity of the air remains close to saturation point.

It is almost impossible to go about in the Rondon Woods for any distance unless a trail is first cut. The steep slope, an indescribable tangle of nearly prone, dripping trees and tough, supple stems draped over a jumble of huge, angular rocks, makes even the open pathway far from easy to navigate. In these residual patches of woods occur trees of the families Palmae, Magnoliaceae, Lauraceae, Guttiferae, Melastomaceae and Compositae, most of which are of gnarled, dwarfed, bent habit, and so tangled together, so coated with orchids and bromeliads, and so blanketed by masses of soaking bryophytes, that the familiar *dictum* must be reversed in this case and one can't see the trees for the wood.

The soil at Rondon is derived both from the underlying diabase and from quartzite. The latter rock, breaking away from the cliffs in huge boulders, is smashed to fragments and forms long screes. Within the forest the soil is almost pure humus but, not being plentiful enough to cover the boulders, merely rests in the interstices between them.

Before the fire this rain-forest formed an unbroken belt completely encircling the mountain. Now, only small patches of woods remain, and they are mainly in the deep valleys where a maximum of humidity obtains. Such forested patches appear to be uniform in character and are very rich in botanical species. The trees, usually gnarled and bent, seldom attain a height of more than thirty feet. They grow outward from the plane of the slope, sending their roots far down among the crevices between the boulders. Small palms form an important feature. Two species of bramble (*Rubus*), both producing delicious blackberries, grow somewhat sporadically on and near the ledge. The fruit is ripe at the beginning of December.

In its lack of coriaceous leaves and inability to guard against loss of moisture, the foliage of Rondon Camp resembles normal cloud-forest foliage of the Andes and elsewhere in the tropics. The leaves wilt and dry readily, and the possibility of destruction in time of drought is very great. Epiphytic plants, orchids, *Brocchinia*, ferns, mosses and Jungermanniaceae form festoons from branch to branch, or spread out in seemingly secure flat mats of verdure through which one may plunge waist deep. At the edges of brooks small differences in the flora can be noted; *Bromelia* and *Brocchinia* seem rarer, and certain hydric forms like filmy-ferns, water-mosses, and Marchantiaceae become numerous. Since the fire a definite replacement flora composed chiefly of mosses, ferns and Compositae has appeared.

The fauna of Rondon Woods, excepting mammals and reptiles, is rich and a very high percentage of the forms are endemic. Many species of birds are represented which, though not common, are inquisitive and unafraid. Mammalian species are limited to three: *Thomasomys macconnelli*, *Zygodontomys*, and a black-spined *Proechimys*, the last very rare. Neither reptiles nor amphibia were noted.

Most of the insects captured were nocturnal forms, chiefly Noctuidae that were attracted by light. By turning over rotting logs in the hill-side forest

Isopoda, Myriopoda, spiders, scorpions, and Solpugida were obtained. A shell-less pulmonate snail (also at Philipp Camp) was plentiful. Two small-shelled snails and several Nematoda about an inch in length were secured.

SUMMIT CAMP, 8600 FEET

One of the first things we did, after making camp on the plateau, was to climb one of the higher morros and look about us. The general impression gained is of a huge stony plain, rutted and fissured, with occasional lighter colored, level sandy areas on which tiny scattered plants are growing. Most of the summit is cold bare rock, the only exception being along the comparatively sheltered sides and in rifts and cracks of the morros. Such areas are clothed with an assemblage of tough, wiry brush growth, among which are *Ilex*, *Bejaria*, *Cyrilla*, *Phoradendron*, *Myrcia* and many others. In a few instances small trees, *Didymopanax*, *Stiftia*, from 4 to 10 feet high occur. A great number of herbaceous forms—orchids, *Heliamphora*, *Mikania*, a lily among them—are intercalated with the heathy growth.

The surface of the plateau, although it appears level when viewed from a distance, is really fretted and scoured by water into a confusion of sandstone mesas and hummocks of all shapes and sizes (fig. 12). When clambering over rocks and crossing rifts considerable risk of injury is incurred through slipping on the film of blackish algae with which the stone is coated everywhere. That part of the summit in the immediate vicinity of the top of the inclined shelf (the only pathway of ascent) is particularly broken up, and is surrounded by great "morros" or more or less isolated, mesa-like rock masses. The rest of the tableland, in addition to the usual jumble of stony hummocks, has deep rifts or fissures crossing it at intervals. A sandy swamp (fig. 11) about 150 yards long covered with tussocks of herbs lies near the centre. The climate is cold and very wet, for the sun shines for only a few hours or less daily. At night strong winds sweep the top of the mountain.

Vegetation in this remarkable region is of necessity highly peculiar, being adapted to grow upon shallow wet sand, on barren rocky surfaces, or in cracks and sheltered places containing some slight assemblage of humus. Such habitats are readily classified.

Open, alga-coated rock surface, almost devoid of higher vegetation, is dominant, and constitutes probably 90 per cent of the total area of the plateau.

Sandy swamps have already been referred to, but there are many smaller tracts. All are approximately level, generally water-saturated, and productive of scattered small plants. Both here and in the following class of swamp the lesser herbs, probably to avoid frequent shallow flooding by rain, are raised up on their roots or stems so that the whorl of basal leaves is maintained an inch or so above the surface of the ground, giving them a stilted

appearance. Plants with this habit of growth are *Paeplanthus*, *Drosera*, sedges, etc.

Humus bogs form in water-filled depressions among the rocks. One of the largest is near the top of the "ledge." They are rich in number and variety of plants, and grade imperceptibly into the next class. A characteristic small tree and the one which furnishes the only firewood on the mountain top, *Bonnetia roraimae*, is usually plentiful. Its roots are buried in water-soaked sphagnum moss.

Small gullies, sheltered, rocky sides of morros and any places where soil has accumulated, but which are not swampy provide the habitat of the majority of the plants and animals recorded from the summit of Roraima

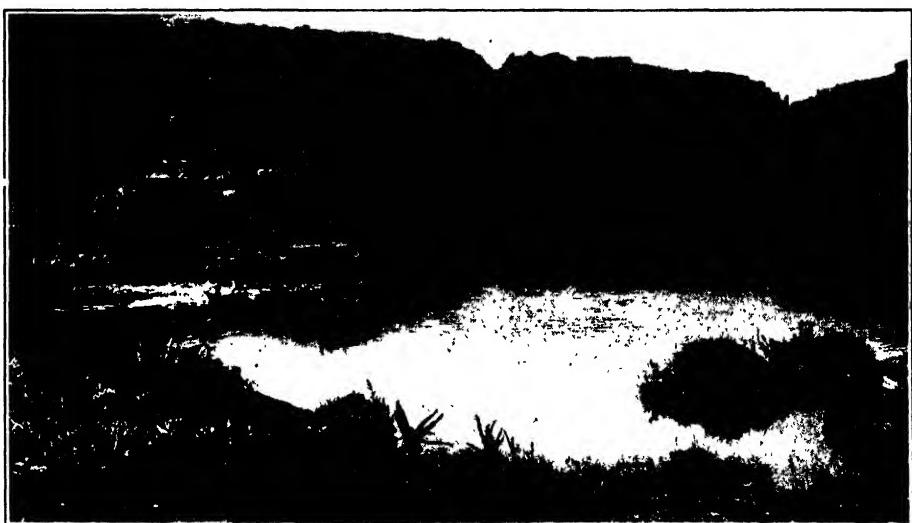


FIG. 11. A pond among the rocks to the northeast of Summit Camp containing numerous dragonfly nymphs. The white dots are reflected light from *Rapatca* leaves.

(fig. 12). In these spots the prevailing vegetation is bushy or heathy, with tough, matted stems and small leaves. The large, pink-flowered, *Rhododendron*-like *Ledotheamnus* grows here.

A distinct rock-wall, or shallow cave flora, occurs, which comprises among other things the fern *Trichomanes*, a crimson-flowered member of the *Lentibulariaceae* (*Orchylillum quelchii*) and many kinds of liverworts and mosses.

The last two habitats offer not only the principal food supply for most of the fauna, but give shelter from climate and from natural enemies. Consequently, almost all of the zoological material collected came from them.

A small quantity of pitcher-plant fluid was collected and suitably preserved. It has recently been tested for enzymes, but with negative results. This is not so very surprising when the degree of dilution by rain is kept in mind. The leaves have an interesting device for regulating the quantity of

water in the pitcher. Each is pierced by a small pore in the seam of the leaf a little below the level of the hairy portion.

Although rather rich in small invertebrates, the summit harbors very few vertebrate animals indeed. Actually only four species of birds appear to be residents, although seven other kinds were observed, and probably visit continually from the rainforests on the slopes below. Among them are finches, *Diglossa major*, a flycatcher, a wren, a hummingbird, a parrot, and several hawks.

Thomasomys macconnelli, a species of mouse discovered by Quelch and known only from the single specimen which he found drowned in his water-bucket, is rather common. In two weeks 25 to 30 specimens were taken. A



FIG. 12. The summit of Roraima near camp with *Rapatea*, *Bromeliaceae*, etc., in the foreground.

few of the females had embryos (November). They appear in no way different from those trapped at Rondon Camp at the foot of the cliffs. Another kind of mouse (Anthony, '29), which has proved to be new and has recently been described, is represented by three males and two females. It appears to be allied to *Oxymycterus* of the southern Andes and south Brazil and has semi-fossorial habits, living in deep tunnels among the sphagnum moss and mat vegetation. The eyes are much reduced in size, and the claws very long; the snout is tapered and shrew-like. No trace was found of it elsewhere than on the plateau. A coatimundi (*Nasua*) was reported by Indians on the summit. They declared that it disappeared quickly among the rocks. Quantities of old droppings of these animals composed mainly of beetle elytra were discovered under sheltered rocks.

No reptiles were discovered; but Quelch took the only known specimen of *Euspondylus leucostictus* Boul. on the plateau. A small toad, *Oreophrynella*

quelchi Boul., slaty black on the back, and having the belly either dark grey or bright orange, is widely distributed all over the plateau, but apparently does not descend to the forests below. It is unable to leap, but crawls slowly and awkwardly among the slippery rocks. When alarmed it releases its hold of the stones and rolls down into cracks or pools, where it "plays 'possum." Nothing was discovered about its breeding habits.

Approximately the following numbers of species of invertebrates were secured: 10 Arachnida, 4 Myriapoda, 1 "lacewing," 2 Collembola, 3 Orthoptera, 2 Odonata, 1 Trichoptera, 1 Psocidae, 2 Henniptera, 2 Homoptera, 1 "thrips," 7 diurnal and 27 nocturnal Lepidoptera, 28 Coleoptera (9 Chrysomelidae), more than 20 Diptera, but only 1 Hymenopteron (a parasitic wasp). Most of these have yet to be determined.

Ants, Mollusca, Crustacea, Scorpionida, and worms (except a leech in the fluid of the pitcher-plant, *Heliamphora*) appear to be absent from the table-land.

Vegetation is tightly packed together on the slopes, in the humus bogs, and in protected spots near the "morros." Compact cushions of Bromeliaceous plants, tussocks of pitcher-plants, *Xyris*, and *Paepalanthus* combine to form a plant association through which small mammals drive their run-ways and lesser creatures seek their food. Among the bushes almost voiceless birds hop quietly. In this world of fog and rain little or no insect activity is noted; but a few moments of sunshine start black butterflies fluttering, gnats dancing, flower-flies and hover-flies buzzing, and great dragon-flies hawking back and forth through the gullies in search of what they may devour.

SUMMARY

The Mt. Roraima region comprises altitudes from 4000 to 8600 feet. The climate varies from 64° at dawn at the lower limit to 52° on the plateau and is found to be progressively more humid as the highlands are approached. Transitions take place from the lower savannas and forests through specialized cloud forest at the base of encircling cliffs, up a narrow inclined ledge to the extensive rocky plateau which is the summit of the mountain. The higher zones in particular contain profoundly modified forms of plants and animals, a large number of which are endemic.

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SUBMERGING EXPERIMENTS WITH *TAXODIUM*¹

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Plant ecologists in general have been interested in two questions concerning *Taxodium distichum* (L.) Richard. Will seeds sprout under water? Will the trees live when completely submerged? The summers of 1927-29 were spent doing field work in the "Sunken Lands" of Arkansas and the region around Reelfoot Lake, Tennessee. These regions were lowered by the New Madrid Earthquake in 1811-12. The St. Francis River in Arkansas was changed from a stream forty to fifty meters wide, flowing in a well-defined channel to a much broader stream, in places reaching a width of five miles, flowing in several poorly defined channels. Water over this region varies from a few centimeters in summer to two to four meters in the spring. As the lower parts fill in with sediment, the river widens each year. Reelfoot Lake, however, has better defined boundaries, due to greater submergence. Here, the great forest areas were lowered about six meters, water from the Mississippi rushing in, entirely submerging the smaller trees and causing death to the largest (Nelson, '24).

How long these big trees survived in six or more meters of water can not be determined. Rowing a boat over the tops of smaller trees and over the huge dead bodies of older ones still standing, which before 1811-12, formed a great virgin forest, is an experience which cannot be duplicated. The parts under water are well preserved. A pole four inches in diameter, after one hundred and twenty years, is still strong enough to wreck a boat. In the lower St. Francis River, the earthquake overturned most of the large trees. The water in Reelfoot Lake is clear, while that in the St. Francis River is very muddy. Before the era of drainage ditches in Arkansas and Missouri, the two regions had similar vegetation. Today, they compare only in their ligneous flora.

We have here a natural made region of known age in the *Taxodium* belt, where, if *Taxodium* seeds will sprout under water and the seedlings live, a great forest should be developing. The only place that we find a forest developing is along the margins of streams, lakes, bayous, or regions flooded for a short time only. Harper ('12) believes that *Taxodium* is rarely or never found on the banks of rivers or other bodies of water which have an average seasonal fluctuation of more than ten or twelve feet.

¹ Paper presented before the Ecological Society of America at New Orleans, December, 1931.

Two sets of experiments, (1) seed submergence and (2) tree submergence, show that seeds do not sprout when submerged and that the trees die when submerged.

SEED SUBMERGENCE

All seeds were collected on the first of November, 1928, from trees growing on the banks of the St. Francis River. They were stored dry in coffee sacks or submerged in water in half gallon glass jars.

Fourteen ten gallon tubs were filled to within five centimeters of the top with soil from under the seed trees.

Tubs 1-4 were placed in a commercial greenhouse in Jonesboro, Arkansas. On November 10, 1928, each tub was planted with about 200 seeds, placed two centimeters deep. Tubs 1-3 were kept filled with water until the first of August, 1929. Tub 4 had holes in its sides and bottom to prevent flooding. No seeds had sprouted in tubs 1-3 by August 1. At this time, the water was poured off but the soil kept moist. By September 26, there was an average of eighteen seedlings in the cotyledon stage in each tub. Tub 4 produced seedlings all through the winter and spring, some by September being 50 centimeters in height.

Tubs 5 and 6 were planted with 200 fresh seeds each, as above, and left in the "sunken lands," where the water was about 25 centimeters deep. Water entered through holes in the sides and bottoms of the tubs. By June 15, tub 5 had 74, and tub 6, 76 seedlings beyond the cotyledon stage.

Tubs 7 and 8 were planted with about 200 seeds each, placed in the "sunken lands," where the water covered the tub at least 30 centimeters deep, from November to April. By June, tub 7 had 68 and tub 8, 73 seedlings.

Tubs 9 and 10 were planted with about 200 seeds each and placed in the swamp where the water was at least a meter and a half deep, from November to July. July 1, not a single seed had sprouted. July 1, tub 10 was removed from the water, but the soil kept moist. On July 15, twenty-four seedlings 5-10 centimeters in height were present. Tub 9, which was kept submerged, had not produced a seedling by September 26.

Tubs 11 and 12, planted with about 200 seeds each on November 10, were placed in water about three meters deep. Tub 11 was in still water which became stagnant by July 1. Tub 12 was in the channel of a drainage ditch where the water was rather swift. No seedlings were produced by September 26.

Tubs 13 and 14, planted November 10 with about 200 seeds each, were placed near the edge of the water where the high water never covered them. A few seedlings were present by the last of June. After sprinkling a few times, many seedlings appeared.

Seeds were also planted in the soil of the river bank in five rows, starting in four feet of water and extending upon a sandy bank four feet above the normal water line. By the last of May, seeds were coming up on the bank

and down to the water's edge. No seeds had sprouted under the water. As the water receded, exposing the soil where the seeds had been planted, seedlings sprang up until the last of September, always keeping close pace with the receding water.

Numerous experiments dealing with only a few seeds were made, with the same results. The seeds stored by submerging in glass jars gave the same results as the seeds stored in coffee sacks. A few seeds planted in moist soil grew after being stored in water thirty months. As the water rises in the flooded St. Francis River basin, and in the regions around Reelfoot Lake, millions of seeds that do not sink are carried from place to place, coming in contact with the soil when the water recedes. Millions of seedlings spring up. Never do the seeds sprout in the above regions under permanent water.

SUBMERGING TAXODIUM

As mentioned above, submerging trees in water to a depth of six meters in Reelfoot Lake and the Lower St. Francis River resulted in their death. When the water is only two to three meters deep, most of the trees are still alive, but have dead branches in their tops. These are pictured very well by Nelson ('24). Where the water is only one half to two meters deep, they thrive much better. The water in Reelfoot Lake is shallow in many places, seldom reaching six meters during normal rainfall.

Seedlings, ranging in age from the cotyledon stage to four years old, were submerged in a number of experiments in the St. Francis River, to see how long they would live, if at all. Present-year seedlings were transplanted into tubs or large buckets and allowed to grow a few days to adjust themselves. If kept moist, they are very easy to transplant. Older specimens had been transplanted the previous year. Table I shows the results of five experiments

TABLE I. *Results of submergence of young Taxodium at four different depths.*

Date of submergence	No. of plants	Depth in water	Result
June 25.....	30	2 meters	July 6—All dead
June 26.....	80	3 meters	July 6—79 dead July 10—All dead
June 26.....	80	1 meter	July 6—80 dead
June 26.....	80	Barely submerged	July 6—80 dead
June 26.....	80	Barely submerged	July 6—78 dead

involving submergence of 350 seedlings 20–30 centimeters in height, submergence varying from three meters to two or three centimeters. All plants were dead within about two weeks. The controls (plants same size, growing in same kind of containers but not submerged), only a few centimeters away, lived.

The above results show that seedlings 20 to 30 centimeters in height die in from 10 to 12 days when submerged.

On July 10, one bucket of twenty-five specimens was sunk in a tub of water. City water was added daily, so that it just covered the entire plants. The water was clear and the place somewhat shaded for a part of the day. On August 1, the plants were still alive, but no growth had occurred. On September 1, all were moribund and by September 25, all had died.

On August 1, twenty-five specimens in the cotyledon stage were placed in buckets and submerged to a depth of six inches in a tub of clear water. Not a single leaf was formed, and in two weeks every plant was dead.

On June 25, two buckets, each containing twenty-five plants in the cotyledon stage, were placed in a tub so that the seedlings in one were about half submerged, while in the other, the seedlings were entirely submerged. On August 10, only three of the submerged plants were alive. No leaves were produced. All were dead by August 15. Seedlings in the cotyledon stage that were about half submerged produced leaves.

August, 1928, was very hot in the sunken lands region. The water between the farm land and the main current of the river became very warm. It was from 20–100 centimeters deep and stagnant. To live in the water, submerged, or otherwise, *Taxodium* seedlings must withstand these high temperatures.

TABLE II. *Results of submerging 100 plants, about 30 cm. in height, in 30 cm. or less of warm water*

Date	Temperature		No. of specimens	Result	Submergence
	Min.	Max.			
August 1.....	80	96	100		30 cm. or less
" 4.....	81	94		100 dead	
" 5.....	80	92	90		
" 6.....	80	90			
" 7.....	—	87			
" 8.....	80	92		59 dead	
" 10.....	81	92		89 dead	
" 12.....	82	92		90 dead	

In the first experiment with 100 seedlings with high temperature, all plants were dead within four days. In the second experiment with 90 plants, the temperature being lower, some of the plants lived longer.

The temperatures were taken by a maximum and minimum thermometer in the water near the plants.

On July 1, seedlings in the cotyledon stage and some 30 centimeters high, were transplanted in such a way that some of each size were submerged. The submerged plants died, while those not submerged grew.

In September, 1928, seedlings two to three years old were transplanted in five tubs and allowed to grow until July, 1929. All made rapid growth since they had no competition. On July 1, 1929, two of these tubs with 25 trees each, were dragged into the St. Francis River where the water, 10–50 centimeters deep, was very still and somewhat stagnant. Since the depth of the river in July fluctuated, the tubs were dragged along the muddy bottom from time to time in order to keep the trees slightly submerged. The same day,

two tubs of twenty-five specimens each, like the above, were put into the main current of the river, but barely submerged. By July 25, the 100 specimens were dead. The plants in the main current had muddy water for a few days. Those in the still water were exposed to a higher temperature.

The above experiments and the observations made around Reelfoot Lake and in various places among the Arkansas lakes, bayous, and the old beds of the Arkansas River, containing over 5,000,000 acres, lead the writer to believe that for any *Taxodium* seedling of the above species to become established in the swamp areas, the seeds must sprout when not submerged, and the seedlings must grow to sufficient height during the first year to stay above the floods except for a very few days during the second year. Dr. Kurz (unpublished data), who has made many observations on *Taxodium adscendens* Brougniart around certain lakes and rivers in the vicinity of Tallahassee, Florida, states that of the many seedlings that spring up every year after the water recedes, all die when submerged. C. C. Deam (unpublished data) reports like findings for *Taxodium distichum* in southwestern Indiana. Should the flood waters be low for two or three years, the plants may grow enough to keep above the water and become established. Ring counts show that *Taxodium* saplings in any group are about the same age, even though they differ in size. In the St. Francis River basin, the region between the levees has few small trees, one to two meters in height. The levees have narrowed the overflow region, causing the water between them to be much deeper, especially during seasons of high water, killing out those trees whose heads do not keep above the water. Regions outside the levees, where little water stands except during very heavy rains, have many young trees. The floods of 1927 carried many seeds far away from the river, greatly extending the *Taxodium* belt. These seeds germinate very easily when the surface water disappears. The most shaded places will show millions of seedlings, but, due to their light requirements, few live into the second year. *Nyssa aquatica* L. and *Taxodium* are spoken of as ecological equivalents in the low lands of Arkansas. They differ much, however, in their light requirements. *Nyssa* will grow in very deep shade, increasing in diameter very much faster than *Taxodium*, with its crown in full sunlight. *Taxodium*, when present in the low lands, is the primary tree. Draining areas where the trees are well established apparently does not hinder their growth. It is, no doubt, an aid. Mattoon ('15) states that a moderate amount of drainage will undoubtedly be as beneficial to cypress as to various other species, when growing in an excess of water. The trees are found in the low lands, not because this is their choice spot, but because of less competition.

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THE EFFECT OF BIOLOGICALLY CONDITIONED WATER UPON RATE OF GROWTH IN FISHES AND AMPHIBIA¹

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INTRODUCTION

The rate of growth of an animal offers an excellent index for the determination of the effect of certain experimental conditions. In his book on Animal Aggregations, Allee ('31) has devoted two chapters to the problem of the effects of crowding on growth, in which he covers very completely the literature dealing with both the beneficial and harmful effects. It may be well to review here briefly papers dealing with fish and amphibia.

Bilski ('21) reported experiments with different numbers of *Bufo* larvae in like-sized aquaria, and with the same number of larvae in different sized vessels. With decreasing volume per animal, he found that there were descending averages of weight increase. The same author in a 1926 paper concluded that there was a greater regeneration of amputated tails of *Rana esculenta* with decreased volume per animal.

Goetsch ('24), experimenting on *Hydra*, *Planaria*, and amphibian larvae, found that while with the two less active forms, food or the concentration of excretory products played the most important rôle, with the amphibia, if food was controlled, the retarding factor seemed to be overstimulation due to confinement in a small space.

Church ('27) and Shaw ('29), in investigating the effect of homotypic conditioning on the rate of growth in fishes, found that when the water was unchanged over periods of ten days or more, the greatest growth occurred in tanks having the smallest number of fish, although there were exceptions to this, particularly in the early stages of long continued experiments.

Kawajiri ('28), studied the influence of population density of fishes on survival rate and rate of growth. He concluded that, for rainbow trout, the survival rate increased and the rate of growth decreased as the number of fry in a box increased.

Adolph ('29) found that with amphibian larvae the maximum growth occurred with a single animal in the largest volume, although conditioned water could favor the growth of the individual. He found less negative effect of crowding in youth. In his 1931 paper, he reported that the deficiency of body weight of the tadpoles, effected by crowding, retarded metamorphosis.

¹ The present investigation was aided in part by a grant to the University of Chicago from the Rockefeller Foundation administered by W. C. Allee.

Carpenter ('30), found that lead nitrate, by reaction with the mucus secreted by the epithelial cells, made a film over the gills of fish which caused death by suffocation. Survival time in a given concentration was directly influenced by the changes in the ratio of volume of solution to mass of animal. Also, survival time was increased for later members of a series allowed to die successively in a given solution, because of precipitation of the metal by earlier members of the series.

Allee and Bowen ('32) in experiments on the protective effects of groups of goldfish exposed to colloidal silver, determined that there was definite group protection, due to the fact that a greater amount of the colloid was precipitated by the greater number of fishes. The amount of silver removed from suspension was found to correspond exactly with that recovered from the precipitate formed by the mucous secretions.

While the majority of the evidence favors the conclusion that homotypic crowding has a deleterious effect on growth, there are certain exceptions which suggest that this may not always be the case. These possibilities were explored in the present work. Certain experiments on heterotypic conditioning were also undertaken.

EXPERIMENTATION

The experiments to be reported fall into three general divisions. The first division covers experiments dealing with the effect of the conditioning of the medium by animals of a different species (heterotypic conditioning) on growth and regeneration. The second covers experiments on the effect of the conditioning of the medium by animals of the same species (homotypic conditioning) on growth and regeneration. The third is on the effect of heterotypic conditioning on the growth of animals subjected to sublethal doses of toxic substances. The last was suggested by certain experiments of Shelford ('17, '18) on stream pollution, in which he found that fish did not show a negative reaction to water containing certain toxic substances; the experiments in division three were planned with a view to discovering the effect of the presence of associated animals.

Fishes and amphibian larvae were used as experimental animals. The fish were of the tropical species *Platypoecilus maculatus* and *Girardinus guppyi*. The amphibia were *Ambystoma*, of two species, *tigrinum* and *maculatum*. The age of the fishes used ranged from one to four or five months. They were hatched in the Whitman vivarium, and kept in stock aquaria, containing sand and plants, until ready for use. They were fed daily during the period of experimentation. The egg masses of *Ambystoma* were collected in the field and brought into the laboratory. The masses were then isolated, so that experimental and control animals could be taken from the same mass. The larvae were used as soon as possible after hatching, except in one case where it was desired to test animals which had been in the laboratory for some weeks. In

all but this one case the tadpoles were subsisting on yolk and hence needed feeding neither before nor during the experiments.

The water used throughout was from the well in the Whitman vivarium. The vessels in which the animals were kept for experimentation were lined with paraffin in every set of experiments except the first one reported. This was done to prevent the growth of algae, and to make possible the replacement of entirely clean linings at desired intervals.

All experiments on fishes were run in the Whitman vivarium, which has an annual temperature range of 19°–26° C., but is usually at 22° C. The tadpoles were kept in the laboratory proper at a room temperature of 22° C.

I. HETEROTYPIC CONDITIONING

To test the effect of the presence of an associated animal on the fish and amphibia, fresh water mussels of the genera *Anodonta* and *Lampsilis* were used. It was not feasible to have the experimental animals directly associated with the mussels, as the slime they produce has definite food value. The procedure, therefore, was as follows: the mussels were isolated in a large container and the water, which had been conditioned for twenty-four hours, was siphoned from this container through filter paper, to remove the slime, then into the vessels containing the experimental animals. The water for the controls stood in a vessel beside that containing the mussels, so that, as they were both allowed to stand an equal length of time before use, there was sufficient opportunity for both to reach equilibrium. In certain experiments, as explained below, the water was aerated. The control water was also filtered in all except the first two sets of experiments reported.

A. Growth

a. *Platypoecilus*

In these experiments assembled aquaria with glass bottoms and sides, holding eight liters of water, were used. Two fishes were put in each experimental and two in each control aquarium. In this set the water for the controls was not filtered. The fishes were fed ten milligrams of prepared fish food daily. The food was left in for half an hour; at the end of this time all the food which had not been eaten was removed by siphoning. While removing food traces four liters of water were siphoned off, and the aquaria were refilled immediately from the stock containers of conditioned or control water as the case might be. Weekly the aquaria were cleaned and the water was changed entirely. The fishes were measured at the beginning of the experiment and at the end of thirty days. They were measured by putting them in a miniature aquarium whose sides were microscope slides, five millimeters apart, with a millimeter rule fastened to one side. Thus confined, the fishes soon became quiet, and measurements were read with a hand lens, with an experimental error of 0.1 mm. Weighing was not possible since the handling necessary to such a process kills these fish.

The results of these experiments will be found in table I (series I). At the end of the thirty days the average percentage increase was 6.3 per cent for those in conditioned water, and 2.7 per cent for those in unconditioned water. The twenty-one cases give a statistical significance by Student's method of .0044.

These results indicated strongly that fish would grow more rapidly in water which had been conditioned in the manner described. In order to test for any possible food value remaining even in filtered mussel-conditioned water, experiments were run just as has been described except that the fish were given no food (series II). The paraffin linings were replaced at the end of fifteen days, in addition to the washing at the end of seven days. If growth were to occur in the experimental tanks, there would be ground for suspicion that the food factor had not been ruled out.

Practically no growth occurred in the twenty cases (*i.e.*, in only four of the forty tanks—three experimental, one control). From an average size at the beginning of 18.1 mm. for the fish in conditioned water and 18.2 mm. for the controls, there was an average decrease in length of 0.7 per cent and 1.9 per cent respectively. This difference is not significant. There did, however, seem to be some slight survival value of the conditioned water, as the experimental fish lived an average of 28 days, and the controls an average of 25 days. This difference is not significant (.7762).

b. *Ambystoma*

The vessels used for the experiments on tadpoles were finger bowls, holding 200 cc. of water, and lined with paraffin. One animal was placed in each bowl. The water used for the experimental animals was aerated while being mussel-conditioned, and was then filtered. The aeration was introduced to improve the condition of the mussels, and was accomplished by bubbling a slow stream of air through the water continuously. The water for the controls was also aerated and filtered, in this and all subsequent experiments involving mussels. These experiments ran for seven days, and the water was unchanged during that time.

As it was desired to have growth experiments comparable with those on tail regeneration, the tail only was measured, after having ascertained that the tail was a reasonably constant fraction of the total length. The measurement was done under the low power of a binocular dissecting microscope, with the animals resting on a thin piece of glass under which was a millimeter rule. The animals remained quiet and the length was measured with certainty to tenths of a millimeter.

The results, seen in table I (series III), show a beneficial effect of conditioned water. In twelve out of fifteen cases the tadpoles in the conditioned water showed the greater increase in tail length; in two cases there was no difference.

B. Regeneration

In all regeneration experiments, the length of the tail was measured first, then approximately the desired amount was amputated; the length of the remaining tail stump was then measured. At the end of the time of experimentation, the total length of the tail was again measured. Thus by subtracting from this the length of the tail stump, the amount of increase was determined.

a. *Platypoecilus*

The tails of the fishes were removed with fine sharp scissors, while they were in the miniature aquarium. This obviated the bad effects, discovered in preliminary experiments, caused by removal from water for cutting. The amount remaining after cutting varied from 0.2 mm. to 1.0 mm. with an accuracy similar to that in all measurements of fishes.

For these and all subsequent experiments on fish, battery jars were used which had a circular bottom six inches in diameter and a height of eight inches. They were lined with paraffin, which was not renewed in the course

TABLE I. *Summary of data on series I to V inclusive*

Series no.	Species used	No. of exps.	Duration	Heterotypic conditioning			Statistical significance		
				Conditioned water	Control	Mean length at start	Mean length of tail stump	Mean per cent inc.	
I	<i>P. rubra</i>	21	30 da.	12.5*		6.3	12.5	2.7	.0044
II	<i>P. rubra</i> (starved)	20	30 da.	18.1*		-0.7	18.2	-1.9	.1054
III	<i>A. tig.</i>	15	7 da.	5.5		28.9	5.5	25.9	.0254
IV	<i>P. rubra</i>	13	14 da.	3.6	0.5	51.0	3.7	40.5	.0076
V	<i>A. mac.</i>	19	7 da.	4.8	1.0	48.7	4.8	42.7	.0006

* Total length (all others tail length).

Expanded tables have been placed in the University of Chicago library. The type of data available can be ascertained from table III, series XIV, which is given in full.

of these experiments. The experiments ran two weeks. The jars were filled to 1700 cc., which was about half full. Two fishes were put in each jar; they were chosen so as to be distinguishable either by size or markings. They were fed prepared fish food daily. An amount in excess of that which they could consume in half an hour was given them. At the end of that time they were removed from the jars with a small net, and put in a dish of clean water. Separate nets were used for experimental and for control animals. The jars were emptied, rinsed repeatedly to remove all traces of food, then filled with aerated water filtered from the stock containers. The fishes were replaced by pouring.

Of the thirteen cases (with twenty-six fishes) twelve showed increased growth in the conditioned water, giving a statistical significance of .0076 (table I, series IV).

b. *Ambystoma*

In regeneration experiments on tadpoles, the tail amputation was done with a sharp knife-needle, under the binocular dissecting microscope. Removal from the water for the few moments necessary seemed to have no ill effects. The length of the tail stumps varied from 0.6 mm. to 1.5 mm., in experiments in heterotypic conditioning.

Of the nineteen experiments of this type on thirty-eight tadpoles, fifteen were positive, two were negative, and two indifferent, showing a great preponderance of evidence for greater growth in the conditioned water. The figure for significance is .0006. The results will be found summarized in table I, series V.

It has been shown, then, that heterotypic conditioning has a beneficial effect on the rate of growth and the rate of tail regeneration in the fish *Platypoecilus*, and the amphibian *Ambystoma*.

II. HOMOTYPIC CONDITIONING**A. Growth**

No work was done on fish in this connection, as this aspect is being covered by other investigations in this laboratory.

Ambystoma

To test the effect of homotypic conditioning, five tadpoles were placed in one of the paraffin-lined finger bowls holding 200 cc. of water. For control, five others were isolated in five similarly treated bowls. The experiments ran seven days with no change of water.

1. In the first set, the water was taken directly from the well-water tap, filtered, and put into the bowls. In examining table II, series VI, we find that there was not much difference manifested between the thirty isolated animals and the thirty animals living in six groups. The figure for significance is .1940, which shows only a slight tendency toward a positive difference. Each pertinent figure in the table is an average for five animals.

2. It was desired to test the responses of animals which had lived several weeks in the laboratory. Such animals were placed, therefore, in experimental conditions similar to those described above; the water was filtered and put into the bowls without being allowed to stand for any period of time before starting the experiment. The results produced under these conditions are summarized in table II, series VII. Each figure is again an average for five animals. There was a decrease in tail length in all but one case, but the decrease was less in the isolated animals in all cases. The significance of the difference is .0230; that is, there is a definite negative effect of crowding on the rate of growth of animals which have been in the laboratory for a considerable period.

3. Following the suggestion from the work of Bilski and Goetsch that the cause of negative effects of crowding was the stimulation produced by tadpoles colliding with each other, or with the sides of the vessels in small volumes, the following experiments were set up: the bowl to contain the grouped animals was divided into five equal parts by netting which permitted the free circulation of water. In the bowls for the controls the netting was so arranged as to set off a space exactly similar to one of the five divisions of the experimental bowl. Both vessels were filled with the same amount of the usual filtered well-water. By this means it was assured that each of the five experimental animals was confined to the same space as each one of the controls, and that the amount of medium per animal was five times as great for the latter. The arrangement also prevented collisions between animals. The thirty animals used showed almost no difference in growth. The difference shown (table II, series VIII) is not significant.

4. It was thought possible that a protective effect of crowding might be manifested with well water taken directly from the tap and not filtered, as there might be slightly harmful substances suspended in this which were removed by filtering. In this set of experiments only two cases of the twelve were indifferent; the rest were positive, giving a significance of .0002. Each pertinent figure (table II, series IX) is an average for five animals. These experiments are of especial interest, as they very strongly indicate that under certain conditions crowding has a beneficial effect on growth in tadpoles.

B. Regeneration

a. *Platypoecilus*

In these experiments the effect of conditioning was tested by the use of conditioned water instead of by crowding, since the conditioned water method had proved more effective in certain experiments on growth in fishes. A large stock aquarium, lined with paraffin, was filled with thirty-four liters of water, and about thirty fishes (*Platypoecilus*) were put in it. Water for the controls was in another paraffin lined container. Both control and conditioned water containers stood a day before the experiment was begun. The water was then siphoned from the stock containers into paraffin lined battery jars, which contained the fishes used for the experiment. The battery jars were filled to 1700 cc., and the two fishes placed in each. The procedure for feeding and change of water was similar to that described for the experiments on the effect of heterotypic conditioning. The amount of water taken from the stock experimental tank daily, for the renewal of water in the jars, was about half the amount present; the stock fishes were fed and the water completely renewed at the end of a week. Aeration was not necessary in order to keep the fishes in good condition (as had been the case with the mussels, which are stream forms) and the water was not filtered.

TABLE II. Summary of data on series VI to XIII, inclusive

Series no.	Species used	No. of expts.	Duration	Isolated		Homotypic conditioning		Grouped		Statistical significance	Remarks
				Mean tail length at start	Mean tail length of tail stump	Mean per cent inc.	Mean tail length at start	Mean length of tail stump	Mean per cent inc.		
VI	<i>A. tig.</i>	6	7 da.	5.1	31.3	5.1	34.4	34.4	.1940	Young larvae, filtered water	
VII	<i>A. mac.</i>	8	7 da.	6.9	-4.6	-	-11.5	-	.0230	Older larvae, filtered water	
VIII	<i>A. tig.</i>	15	7 da.	4.8	38.2	4.8	40.6	43.70	.0002	Young larvae, filtered water, in frames	
IX	<i>A. tig.</i>	12	7 da.	5.7	5.7	5.6	10.1	10.1	.0002	Young larvae, untreated water	
X	<i>P. rub.</i>	11	14 da.	5.0	0.8	44.0	5.0	36.0	.0158	Untreated water	
XI	<i>A. mac.</i>	10	7 da.	6.9	1.0	28.2	6.9	1.0	.0008	Untreated water	
XII	<i>A. mac.</i>	10	7 da.	6.3	1.0	34.6	6.3	1.0	.0128	Filtered aerated water	
XIII	<i>A. tig.</i>	7	7 da.	5.9	0.9	24.7	5.9	0.9	.0010	Untreated water	

The experiments of series X, involving twenty-two fishes, ran two weeks. The length of the tail stumps varied from 0.3 mm. to 1.1 mm. The measurements at the end showed that all the fishes in conditioned water had grown more than their controls (see table II). The figure for significance is .0158, which indicates that homotypic conditioning has a positive effect on regeneration.

b. *Ambystoma*

In these experiments five animals were grouped in one finger bowl and five isolated in five bowls, as has been previously described in experiments where no frames were used.

It had been necessary to use both *A. tigrinum* and *A. maculatum* in the experiments on the effect of homotypic conditioning on growth. It was thought that the species were sufficiently closely allied so that they would give comparable reactions to experimental conditions. When the first experiments on regeneration were completed, in which *A. maculatum* had been used, it was found that there were enough fresh *tigrinum* on hand to repeat what had been done. This comparison would offer a good test for the above assumption.

No further detailed description is needed of the method employed in these experiments. The manner of tail amputation has been described in a previous section, and the animals were grouped as stated above. The length of the tail stumps varied from 0.8 mm. to 1.2 mm.

The first set (*A. maculatum*, series XI) was in well-water taken from the tap without aeration or filtration. Nine of the ten groups of five showed a higher rate of regeneration than their controls. The significance is .0008.

The second set (series XII) was in filtered and aerated water. A similar result occurred here, giving a significance of .0128. Considering the two sets together, there is almost no statistical chance that the results lack significance.

The conditions for the *tigrinum* experiments (series XIII) were a repetition of those for the first set of *maculatum* experiments, in untreated well-water. All the grouped animals showed a greater increase in growth than the controls. The statistical significance is .0010. These results are in close agreement with those given above for *maculatum*, which offers support for the assumption that the two species react similarly to these experimental conditions.

The results of these three sets of experiments are summarized in table II under the series numbers XI, XII, and XIII, where each pertinent figure represents an average for five animals.

This group of experiments indicates that crowding has a beneficial effect on the rate of tail regeneration.

III. TOXIC SOLUTIONS

A. *Platypoecilus*, in solutions of $HgCl_2$

Preliminary trials were made to determine the lethal dose of mercuric chloride. As was expected, it was found to be exceedingly toxic. No fishes which were tried lived for thirty days in a concentration above that made by adding one cc. of .001 saturated (9.2×10^{-6} N) $HgCl_2$ to 3400 cc. of water (i.e., 2.71×10^{-8} N). Some lived for as much as fifteen days, but no more, in slightly stronger concentrations. In the seventeen experiments run, varyingly weaker concentrations were used, in the attempt to make conditions more favorable for positive growth, for, as will be seen from inspection of table III, series XIV, the majority of the fishes showed a decrease in length.

TABLE III. Series XIV

Fish pair no.	Conditioned water		Control		Saturation of $HgCl_2$ added	Normality of $HgCl_2$
	Length at start	Per cent increase	Length at start	Per cent increase		
1	18.8	0.5	19.2	0.0	.001	9.2×10^{-6}
2	19.0	0.0	19.1	0.0	.0005	9.2×10^{-6}
3	17.2	-1.7	17.3	-4.6	.0005	
4	18.0	2.6	18.0	0.0	.0001	4.6×10^{-6}
5	17.9	0.0	19.0	0.0	.0001	
6	18.2	-1.0	18.5	-3.2	.0001	
7	18.5	-2.7	19.6	-4.0	.0001	
8	15.4	-0.6	15.4	-2.6	.000025	2.3×10^{-7}
9	20.2	-1.0	20.5	-2.4	.000025	
10	16.0	-0.6	16.5	-3.0	.000025	
11	15.1	0.0	14.2	0.0	.000001	9.2×10^{-8}
12	10.8	-5.5	10.0	0.0	.000001	
13	10.5	2.7	9.0	0.0	.000001	
14	16.3	4.9	16.5	2.4	.000001	
15	10.0	3.3	9.8	-3.1	.000001	
16	10.7	0.9	9.0	0.0	.000001	
17	14.0	3.6	14.3	-0.7	.000001	
Mean:	15.7	0.4	15.6	-1.2		
Statistical significance:		.0194				

Of the eight fishes out of the thirty-four which did show an increase in length, six were in tanks having the least amount of poison added.

Two fishes were put in each paraffin lined jar. These jars held 3400 cc. Mussel-conditioned water was aerated and filtered into the experimental jars and unconditioned water was similarly treated for the controls. One cc. of $HgCl_2$ solution of the desired strength was added at the beginning of the experiments. The water was half changed daily. At the time the change was made, the fishes were removed and put into paraffin lined dishes for feeding. An amount of food was given them slightly in excess of that which they could consume in a half hour. At the end of that time, the fishes were transferred into dishes of clean water, from which they were again removed in a few minutes and replaced in the battery jars. One half cc. of the proper

concentration of $HgCl_2$ was then added. The jars were washed and the water completely changed weekly. The experiments ran for thirty days.

The average percentage increase for the seven experimental fish showing an increase in length was 2.6 per cent. Only one control fish showed an increase. The table below, given in full to show concentration used in each case, shows that the average percentage increase for all seventeen experimental fishes was 0.4 per cent, and for all the controls, — 1.2 per cent.

B. *Girardinus guppyi* in solutions of NH_4Cl

Experiments on this substance were added, since it occurs in industrial wastes.

The same procedure was followed in these experiments as in those on $HgCl_2$. One cc. of .01 concentrated (10 g./L., or .1868 N) NH_4Cl was added at the beginning of the experiment of 3400 cc. of water, and one half cc. replaced daily, with the half changes of water. Ten of the twenty-two fishes (series XV) showed an increase of growth; nine of these ten were in conditioned water. From a mean length at the beginning of the experiment of 12.0 mm. for the fishes in conditioned water and 12.3 mm. for the controls, the former showed a mean increase of 2.9 per cent, and the latter of — 2.2 per cent. This gives a statistical significance of .0030.

These experiments indicate that the presence of an associated animal of a different species may have the effect of favoring growth in media containing sublethal amounts of toxic substances.

CONCLUSIONS

I. In a medium of filtered mussel-conditioned water, as contrasted with non conditioned filtered water, there is:

- A. Greater growth in
 - a. *Platypocilus rubra*.²
 - b. Larvae of *Ambystoma tigrinum* (uncut tails).
- B. More rapid regeneration of amputated tails in:
 - a. *P. rubra*.
 - b. Larvae of *A. maculatum*.

II. In homotypically conditioned water, as contrasted with non-conditioned water, there is:

- A. As regards growth in groups as contrasted with isolated individuals,
 - 1. Greater increase in the length of uncut tails in *A. tigrinum* in unfiltered, but not in filtered water.
 - 2. Greater decrease in the length of uncut tails in *A. maculatum* in filtered water, when the animals have been in the laboratory several weeks.

² Non-conditioned water unfiltered in experiments shown in series I.

3. No difference, in filtered water, when the available space remains the same, and the available volume is five times as great for the isolated animals as for the groups, and the animals are prevented from coming in contact with each other.
- B. More rapid regeneration of amputated tails in:
 - a. *P. rubra* (conditioned water, not grouped).
 - b. *A. maculatum* in untreated, and also in filtered and aerated water, and *A. tigrinum* in untreated water (grouped).

III. The presence of mussels has a beneficial effect on the growth of fish in water to which a sublethal dose of $HgCl_2$ or NH_4Cl has been added.

DISCUSSION

We are more familiar, perhaps, with the occurrence of beneficial effects of heterotypic conditioning in nature, than of homotypic conditioning; in fact, the latter has usually been found to produce harmful results, particularly if over-crowding prevails. The phenomena of ecological succession give many supporting considerations for this point of view. In the upland forest succession in sand, the oak associates grow up where the pines have formed sufficient shade and humus, and they, correspondingly, must give way to the beech-maple climax, for they have made changes in the environment unsuitable for themselves, but beneficial for other species which enter as a succeeding stage in ecological succession. The beech-maple forest forms a so-called climax stage in which the forms present no longer produce conditions toxic to themselves. Subject to climatic control such communities exist for long periods, and whatever changes are made in the environment are at least not detrimental to the continued existence of the community.

Such considerations suggest that there are probably many instances where the presence of different species may serve a useful end, to one where the effect of the presence of numbers of the same species is beneficial. Experiences in the course of the present work have tended to support such a difference in emphasis. Clear evidence regarding the beneficial effects of heterotypic conditioning was obtained with a great deal less preliminary exploration than that pertaining to homotypic conditioning. A number of paths of approach, which proved to be blind alleys, were tried, in attempting to find whether there were circumstances under which homotypic conditioning would give positive results. The controlling factors, it seemed, were complex. Preliminary work had mainly to do with various volume relationships. Heterotypic conditioning, on the other hand, was found to have positive effects in much more nearly the first situations tried, which would indicate that the effect was more widespread. It may be that while numbers of the same species may alter the environment in a beneficial direction in a manner quite comparable to that of numbers of a different species, the changes produced in the water by homotypic secretions or excretions or their decom-

position products are more toxic than are those of other species. Thus a nicer balance must be struck, in such matters as volume relationships and frequency of change of medium, in order to realize the possibilities of obtaining positive effects by homotypic conditioning. In this connection there is the work of Woodruff ('14), who found that the excretory products of Paramecia are toxic to themselves, and that this is also true of hypotrichs. The excretory products of hypotrichs, however, stimulate the reproductive rate of Paramecia, which normally succeed them in protozoan succession.

There was one exception, however, to this general point of view. This occurred in the experiments on the effect of homotypic conditioning on the tail regeneration of tadpoles. In twenty experiments on *A. maculatum*, the chances of random sampling giving so great a difference between experiment and control were practically zero, and it took only seven experiments on *tigrinum* to give a statistical significance of .0010. Besides the fact that these two experiments are among the most clearly significant, statistically, of the entire series reported, the results were obtained after very little preliminary work. They are comparable, therefore, to the type of growth response exhibited to heterotypic conditioning of experimental water. The less elusive evidence for positive effects of homotypic conditioning on regeneration may be due to the fact that the body fluids exuding from the cut surface have a more beneficial effect upon a wounded surface than the secretions or excretions from the normal animal have upon growth. With a number of animals present, the salt and organic content of such an exudate, going into the surrounding medium, would tend to bring the medium into balance with the body fluids of the animals more quickly than they would in the case of the isolated animals.

The growth responses shown by tadpoles to homotypic conditioning are of interest from the standpoint of previous work done in this line. In Bilski's work, from which he concluded that crowding has a deleterious effect, the tadpoles he used had been in the laboratory for a week before he separated them for his experiments, which ran for over a month. Goetsch gives the length of his axolotl larvae as 15 mm. Of the experiments reported above, the set most comparable in age of larvae is that summarized in table II, series VII, which gives results on animals three or four weeks old at the beginning of the seven day experiment in filtered water. As we have seen, these showed a definite negative response to conditioning. Two sets, also in filtered water, showed an indifferent response—one in which network partitions separated the available space from the available volume of water, and prevented collisions between animals, and another without such a network. The conditions under which a definite positive effect of homotypic conditioning was demonstrated included unfiltered water and very young larvae. It seems reasonable to suggest, in the light of these results, that the age of the larvae and the exact composition of the medium may be important factors in determining the effect of homotypic conditioning.

Situations in nature come easily to mind in considering the possible usefulness of a positive effect of heterotypic conditioning. The stream from which the mussels were collected is inhabited by a number of species of small fish. It is quite likely that the presence of the molluscs adds definitely to the favorableness of this stream as a fish habitat, while the well known relation between fishes and pelecypod glochidia makes fish occupancy a necessary prerequisite for these fresh water molluscs. Examples of this sort are easily multiplied. The practice is commonplace of placing snails in aquaria with fish, in order to secure better living conditions for the fish. Quite a parallel suggestion to the above is obvious in reference to experiments involving toxic materials. Although these fresh water mussels are not found where the concentration of industrial wastes is high, there are two possibilities in this connection: first, that the mussels may be positively effective either by conditioning the stream above the point where the wastes are added, or further down stream where the concentration is low enough for them to live; and second, that the presence of other species which can exist in a higher concentration may show the same beneficial effect of heterotypic conditioning as has been found for mussels.

While the positive effects of homotypic conditioning on growth do not seem to be so widespread, they may be equally important where present. The previous work in this laboratory (Allee, '31), and elsewhere, upon the beneficial effects of homotypic crowding in clearing up toxic solutions, so that all or the majority of animals in a group may survive under conditions which would kill isolated animals, indicates that in newly evolved or in polluted environments homotypic conditioning may have significantly beneficial effects.

The absence of harmful effects, which was observed in all experiments except those on older tadpoles, shows that under the conditions of these experiments the animals can tolerate the proximity of other similar animals in the same restricted area. This means that the well known adverse effects of homotypic crowding can be avoided more easily than the beneficial effects can be demonstrated. Such a neutral zone corresponds to the first level of social organization (Allee, '31), the toleration level.

The next question to be answered experimentally concerns the possible mechanism by which the effects of conditioning are produced. There are two broad divisions here; first, is there a removal of toxic material from the well-water used, or, second, is there an addition of a growth promoting substance? In one set only of the above experiments do we find any facts which might bear on this question. Tadpoles in filtered water did not show any significant difference between groups and singles, but those in untreated water did. This suggests that the removal of toxic material by the crowding animals is the effective agent in promoting growth of these tadpoles and that such removal may be accomplished by filtering as well. In connection with the experiments on fish in toxic solutions, the findings of others would indi-

cate that toxic material was being removed; however, no direct tests were made on this point in these experiments.

Further, it is worth pointing out that in all experiments on heterotypic conditioning, and in those on homotypic conditioning in fish, the animals were isolated or in twos, rather than in larger groups. This limits the manner in which the experimental animals could be affected differently from the controls to some change made in the medium, and excludes any mechanism involving direct interaction between the animals, such as is concerned in Bilski's stimulation factor.

Chemical analyses of the water in the Whitman laboratory are in progress, as are also investigations of the protozoan and bacterial content of raw and of conditioned waters. It is to be hoped that these analyses will bring to light just what changes are made in the water by conditioning and will open up opportunities for experimental investigation as to the exact nature of the growth promoting factors in homotypically and heterotypically conditioned media.

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OSMOTIC CONCENTRATIONS OF CHAPARRAL, COASTAL SAGEBRUSH, AND DUNE SPECIES OF SOUTHERN CALIFORNIA

C. J. WHITFIELD

During the winters of 1930 and 1931 a number of ecological investigations were conducted under the auspices of the Carnegie Institution of Washington in the county of Santa Barbara, California. Field work was carried on in the Santa Ynez Range at an elevation of 3100 feet; in the sand dunes along the coast, 14 miles northwest of Santa Barbara city; and in the lower end of Mission Canyon, three miles from Santa Barbara.

Santa Barbara County is bounded on the south and west by the ocean and is crossed by two main mountain ranges. The more prominent group is the San Rafael Mountains, whose peaks vary in elevation from 3000 to 7000 feet. The second group, the Santa Ynez Range, rises directly from the sea to elevations varying from 1000 feet in the west to more than 4000 feet in the east, where it joins the San Rafael Mountains. The Santa Ynez Valley, which separates the two ranges, is a long, narrow valley running westward and ranging in width from a few hundred feet to over a mile.

VEGETATION

Two associations, the coastal sagebrush and the coastal chaparral, are represented in the Santa Barbara region.

There are few publications on these vegetational types. Cooper's ('22) ecological treatment of the broad-sclerophyll vegetation of California is outstanding. Plummer's ('11) paper on the chaparral, while not so extensive as Cooper's, gives a good idea of the composition, range, and value of the climax species of this association.

All five of the characteristic species of the coastal sagebrush association, *Artemisia californica*, *Salvia mellifera*, *S. leucophylla*, *S. apiana* and *Eriogonum fasciculatum*, are represented in this region. They are to be found at practically all elevations, but reach their greatest abundance along the coast and in the lower foothills. All but *S. apiana*, which is of secondary importance, attain sufficient numbers to dominate these lower areas.

The conspicuous and important vegetational unit is the coastal chaparral association. The dominant species of this association in the Santa Barbara region are *Adenostoma fasciculatum*, *Arctostaphylos glauca*, *Ceanothus diversifolius*, *C. crassifolius*, *Cercocarpus parvifolius*, and *Quercus dumosa*. All of the coastal sagebrush dominants, but more especially *Artemisia*, *Eriogonum*, and *S. mellifera*, are closely associated in abundance with the characteristic chaparral species. The sagebrush species extend from the coast through-

out the chaparral, and many of the chaparral species extend from the mountains to the coast.

The Santa Ynez range is almost entirely covered with chaparral (figs. 1, 2). A few pines, *Pinus coulteri*, are scattered on the highest points, and *Umbellularia californica* and *Platanus racemosa* occur in draws, ravines, and on north slopes. *Quercus agrifolia*, the conspicuous and important tree of the region, is widespread and abundant, occurring more commonly in less exposed situations.

Of the chaparral species *Adenostoma fasciculatum* is probably the most abundant and widespread. This species occurs in pure stands or mixes with other species, in all conditions, from the coast to the tops of the mountains. Closely associated with *Adenostoma* are *Arctostaphylos glauca* and various species of *Ceanothus*. *Arctostaphylos* is limited to the upper foothills and higher slopes, where, although seldom occurring alone, it forms a conspicuous element of the vegetation. *Ceanothus crassifolius* is especially abundant on the mountains, and with *C. divaricatus* and *C. cuneatus* forms an important part of the chaparral. The significance of the genus *Ceanothus* is shown by the fact that Clements ('20) lists the coastal chaparral as the "Adenostoma-Ceanothus Association." *Quercus dumosa* is a conspicuous species. It is widespread, especially at higher elevations, ranking next to *Adenostoma* in abundance, and growing in all conditions of slope and exposure. *Cercocarpus parvifolius* var. *betulaefolius* is also common, occurring in the more xeric situations throughout the mountains down to an elevation of approximately 200 feet.

A number of species some of which may dominate in other regions are only of secondary importance here. The most conspicuous of these are *Arctostaphylos manzanita*, *Ceanothus spinosus*, *Dendromecon rigidum*, *Eriodictyon californicum*, *Heteromeles arbutifolia*, *Malvastrum fremonti*, *Prunus ilicifolia*, *Rhamnus californica*, *Rhus diversiloba*, *R. integrifolia*, *R. laurina*, *R. ovata*, and *Yucca whipplei*.

Other species frequently met with and of less importance are *Clematis ligusticifolia*, *C. lasiantha*, *Ribes speciosum*, *R. malvaceum*, *Romneya coulteri*, *Senecio douglasii*, *Venegasia carpoides*, *Gilia californica*, *Malacothrix sarratifilis*, *M. tenuifolia*, *Castilleja foliolosa*, *Sphaeralcea calycina*, *Trichostema lanatum*, *Encelia californica*, *Lotus scoparius*, *Echinocystis fabaceae*, *Marubium vulgare*, and various species of *Lupinus* and *Pentstemon*.

The succulent vegetation of the sand dunes is in striking contrast to the sclerophyllous chaparral. Although some chaparral species, such as *Adenostoma*, occur in the sand dunes, *Convolvulus*, *Abronia*, and *Oenothera*, typical dune species, are limited to their own specific habitat. Just back of the shore line *Abronia maritima* is dominant, *A. umbellata* of secondary importance. In lower, saltier areas *Salicornia subterminalis*, *Suaeda depressa*, and *Distichlis spicata* occur. *Distichlis* is quite common well back in the dunes. Near the coast and ocean spray occur such species as *Convolvulus*

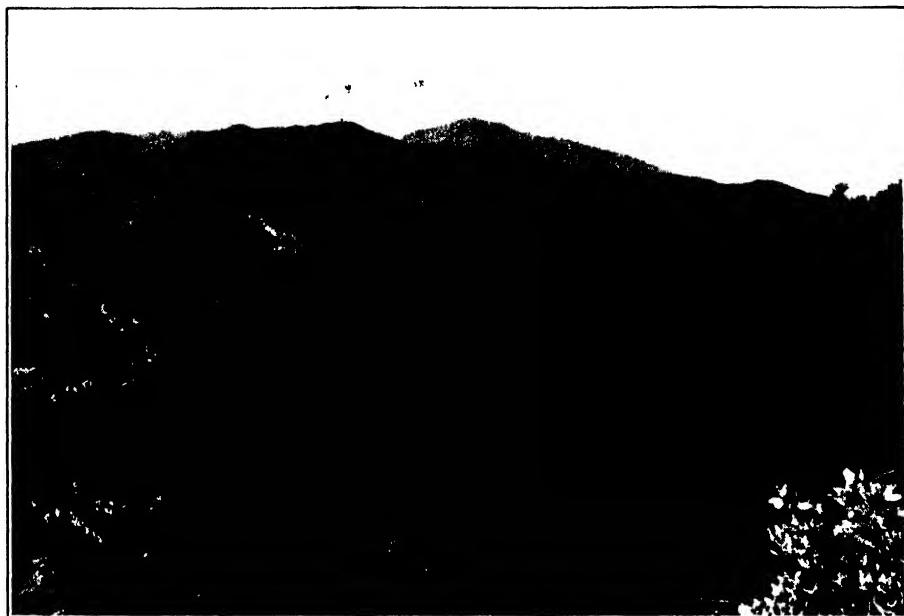


FIG. 1. Slopes of the Santa Ynez Range covered with chaparral.

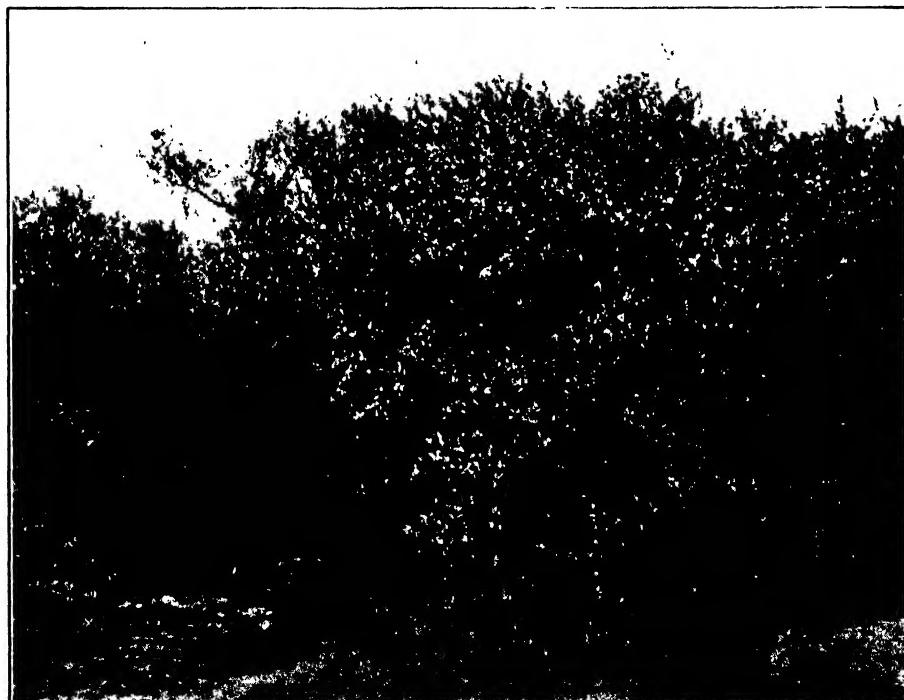


FIG. 2. Coastal chaparral with *Arctostaphylos* sp. and *Quercus dumosa* in the foreground.

soldanella, *Franseria bipinnatifida*, *Oenothera contorta*, *Amsinchia intermedia*, *Malacothrix tenuifolia*, and *Haplopappus ericoides*. Further inland *Lupinus chanissonis*, *Solanum douglasii*, and *Heterotheca grandiflora* are conspicuous, while in depressions *Baccharis pilularis*, *Haplopappus squarrosa*, and *Salix lasiolepis* occur.

FACTORS

The climate of Santa Barbara County is equable throughout the year, excessive heat and cold being very rare. The average winter and spring rainfall from 1928 to 1930 at Santa Barbara was 13.62 inches and at the Santa Ynez station 19.96 inches. The season of 1930-31 was very dry, Santa Barbara receiving only 9.79 inches by April 10.

Transpirational and instrumental studies were conducted at the various stations. During the week of March 2-9, 1931, the water loss at the Santa Barbara station was approximately 14.0 per cent higher than at the dune station (table I). The average day air temperature and average daily relative humidity were approximately similar at the two stations, while the average night air temperature, saturation deficit, and evaporation were higher in Santa Barbara. Wind movement was greater at the dunes. During this period water loss from the plants at the mountain station was practically the same as that of plants at the Santa Barbara station.

A second experiment conducted April 7-10 at the mountain and Santa Barbara stations also showed approximately the same water loss and evaporation (evaporimeter) at both stations (table I). Air temperature, relative humidity, and saturation deficit were higher at Santa Barbara, while atmometer loss and wind were higher in the mountains.

TABLE I. *Climatic observations. Daily averages*

Station	Transpiration, cc. per plant	Air temperature, ° F.		Relative humidity, per cent		Saturation deficit, grains per cu. ft.	Evaporimeter losses, cc.	Atmometer losses, cc.		Wind miles per hour
		Day	Night	Day	Night			White	Black	
Santa Barbara March 2-9, 1931	78	67	52	64	—	1.95	270	29	45	30
Dunes March 2-9, 1931	69	66	45	65	—	1.76	249	23	38	43
Santa Barbara April 7-10, 1931	86	74	58	44	77	2.73	445	36	—	20
Mountain April 7-10, 1931	85	60	47	39	50	2.58	442	49	—	189

OSMOTIC VALUES

Osmotic determinations were made at three different times on approximately twenty species in each of the three communities. The method employed was similar to that used by H. Walter ('29, '31).

The material was selected in order to secure representative species from each of the three habitats, and to secure species which were to be found in more than one of the different communities. The first series of determinations was made during the week ending February 15. In this series mature or maturing leaves were selected in practically all cases. The second set of determinations was made during the week ending April 5. During this period, from February 15 to April 5, rain fell neither in the coastal sagebrush association nor on the dunes, although twice slight precipitation was recorded in the mountain chaparral. While making the second collection it was found that the old leaves of some species had been shed and that new leaves had de-

TABLE II. Freezing points (Δ) and osmotic concentrations in atmospheres of pressure (P) of dune, coastal sagebrush, and coastal chaparral species

		Feb. 15	P	April 5	P	Oct. 10	P
		Δ		Δ		Δ	
<i>Dune Vegetation: Sea level</i>							
1. <i>Abronia maritima</i>	1.061	12.772	1.392	16.744	1.699	20.068	
2. <i>Ambrosia psilostachya</i>	1.221	14.692	2.308	27.726	2.143	25.746*	
3. <i>Amsinchia intermedia</i>	0.947	11.404	1.835	22.060	—	—	
4. <i>Artemisia californica</i>	1.344	16.168	2.281	27.402	—	—	
5. <i>Artemisia vulgaris</i>	1.102	13.264	1.799	20.548	1.235	14.860*	
6. <i>Baccharis pilularis</i>	1.314	15.808	1.583	19.036	1.382	16.624*	
7. <i>Brassica campestris</i>	1.129	13.588	0.986	11.872	—	—	
8. <i>Cirsium californicum</i>	0.828	9.971	1.343	16.156	0.979	11.788*	
9. <i>Convolvulus soldanella</i>	0.949	11.428	0.901	10.852	0.741	8.975	
10. <i>Eschscholtzia californica</i>	1.287	15.484	1.357	16.324	—	—	
11. <i>Franseria bipinnatifida</i>	0.919	11.068	1.314	15.808	0.904	10.888*	
12. <i>Haplopappus squarrosa</i>	1.465	17.620	1.530	18.400	1.807	21.724	
13. <i>Heterotheca grandiflora</i>	0.914	11.008	1.136	13.672	0.773	9.310*	
14. <i>Lupinus chamissonis</i>	1.312	15.784	1.424	17.128	—	—	
15. <i>Malacothrix s. tenuifolia</i>	0.870	10.480	1.193	14.356	—	—	
16. <i>Oenothera contorta</i>	0.998	12.016	0.782	9.418	0.557	6.711*	
17. <i>Phacelia ramosissima</i>	1.252	15.064	1.413	16.996	1.137	13.684*	
18. <i>Salix lasiolepis</i>	1.630	19.600	2.158	25.926	1.589	19.108	
19. <i>Solanum douglasii</i>	0.849	10.228	1.282	15.424	0.874	10.528*	
20. <i>Suaeda depressa</i>	1.870	22.480	3.613	43.296	3.532	42.334*	
<i>Coastal Sagebrush:</i>							
<i>Altitude 200 feet</i>							
1. <i>Artemisia californica</i>	1.289	15.508	1.363	16.396	—	—	
2. <i>Cirsium californicum</i>	0.671	8.083	0.749	9.071	—	—	
3. <i>Ceanothus spinosus</i>	1.221	14.692	1.774	21.328	—	—	
4. <i>Echinocystis fabacea</i>	0.789	9.402	0.772	9.298	—	—	
5. <i>Marrubium vulgare</i>	1.082	13.024	1.277	15.304	—	—	
6. <i>Paeonia brownii</i>	1.523	18.316	1.836	22.072	—	—	
7. <i>Phacelia ramosissima</i>	0.841	10.132	0.876	10.552	—	—	
8. <i>Platanus racemosa</i>	1.028	12.376	1.109	13.348	—	—	
9. <i>Prunus ilicifolia</i>	2.598	31.186	2.213	26.586	2.998	35.966	
10. <i>Quercus agrifolia</i>	1.611	19.372	2.416	29.024	2.364	28.388	
11. <i>Rhus laurina</i>	1.427	17.164	1.711	20.572	—	—	
12. <i>Ribes speciosum</i>	1.186	14.272	1.271	15.292	—	—	
13. <i>Rosa californica</i>	1.284	15.448	1.301	15.652	1.999	24.028	
14. <i>Salvia apiana</i>	1.031	12.412	1.155	13.900	3.097	37.144	
15. <i>Salvia mellifera</i>	0.980	11.800	0.915	11.020	2.783	33.396	
16. <i>Salvia spathacea</i>	1.157	13.924	0.943	11.356	2.244	26.958	
17. <i>Sambucus velutina</i>	1.015	12.220	1.113	13.396	1.394	16.768	
18. <i>Scrophularia californica</i>	1.003	12.076	1.101	13.252	—	—	
19. <i>Solanum douglasii</i>	1.064	12.808	1.071	12.893	1.897	22.804	
20. <i>Venegasia carpesoides</i>	0.826	9.947	0.961	11.572	—	—	

TABLE II.—Continued

	Feb. 15 Δ	P	April 5 Δ	P	Oct. 10 Δ	P
<i>Coastal Chaparral:</i>						
Altitude 2600 to 3100 feet						
1. <i>Adenostoma fasciculatum</i> ...	2.280	27.390	2.302	27.654	2.787	33.444
2. <i>Arctostaphylos glauca</i>	2.277	27.354	2.154	25.878	3.097	37.144
3. <i>Artemisia californica</i>	1.383	16.636	1.702	20.464	—	—
4. <i>Ceanothus crassifolius</i>	2.270	27.270	1.899	22.808*	—	—
5. <i>Ceanothus spinosus</i>	1.898	22.816	1.754	21.088	—	—
6. <i>Dendromecon rigidum</i>	1.395	16.780	1.327	15.964	1.543	18.556
7. <i>Echinocystis fabacea</i>	0.838	10.097	0.907	10.924	—	—
8. <i>Heteromeles arbutifolia</i>	2.178	26.166	2.320	27.870	2.721	32.662
9. <i>Paeonia brownii</i>	1.575	18.940	1.527	18.314	—	—
10. <i>Prunus ilicifolia</i>	2.842	34.104	2.794	33.528	3.989	47.778
11. <i>Quercus agrifolia</i>	2.503	30.056	2.144	25.758	2.321	27.882
12. <i>Quercus dumosa</i>	2.326	27.942	1.265	15.220*	2.416	29.012
13. <i>Rhus ovata</i>	2.138	25.686	2.288	27.486	—	—
14. <i>Ribes malvaceum</i>	1.555	18.700	1.464	17.608	—	—
15. <i>Ribes speciosum</i>	1.836	22.072	1.556	18.712*	—	—
16. <i>Salvia mellifera</i>	1.328	15.976	1.318	15.856	1.496	17.992
17. <i>Salvia spathacea</i>	1.258	15.136	1.103	13.276	1.668	20.056
18. <i>Sambucus velutina</i>	1.079	12.988	1.318	15.856	1.381	16.612
19. <i>Trichostema lanatum</i>	1.238	14.896	1.236	14.872	1.185	14.260
20. <i>Umbellularia californica</i> ...	2.236	26.862	2.281	27.402	2.377	28.544

veloped. This phenomenon was most conspicuous in the coastal chaparral. As young leaves of the same species have lower values than old leaves, these individuals consequently gave lower values. Those species in which the development of new leaves was apparent are indicated by asterisks. The material for the third group of determinations was collected during the week ending October 10. By this date some of the species had dried, while the leaves of others had fallen or were falling. A dash (—) in table II indicates that no material was collected for these species. The dry summer was interrupted by two rains during August, while the fall rains began October 10.

DISCUSSION

The osmotic values of most of the dune species increased from February to April, but were low in October (table I). The dune vegetation in October showed the best growth of any of the three communities. Many of the species, such as *Solanum*, *Heterotheca*, *Abronia*, *Baccharis*, and *Oenothera* were flowering abundantly. The leaves of over half of the species had fallen or were falling, and new leaves had developed. In addition, *Convolvulus* and *Oenothera* showed constant decreases.

The osmotic values of nearly all the species collected in the coastal sage-brush showed a constant increase from February to October. In October this habitat showed the most xerophytic tendencies of all three communities. Some species, as *Salvia spathacea*, *S. mellifera*, and *Solanum douglasii*, were rapidly drying out. Although material was collected, sufficient sap for a determination could not be extracted from the leaves of *Ceanothus spinosus*.

The values for most of the coastal chaparral species were highest in October, and lowest in April. The latter condition is undoubtedly due to the formation of new leaves, as was mentioned before. Conditions were not so xeric in this association as in the coastal sagebrush. As in the sagebrush association, sufficient sap for a determination could not be extracted from the two species of *Ceanothus*.

A comparison of the osmotic values of the same species from different habitats gives an indication of the water conditions of the soils. With only a single exception, all values were higher in the dunes than in the coastal sagebrush in February and April. With the exception of *Artemisia californica* no data are available to show a relationship between the dunes and the coastal chaparral. The results of this single species indicates that the dunes were also more xeric than was the coastal chaparral. In February, the values for plants of the same species were all higher in the coastal chaparral than in the coastal sagebrush, and all but three species had higher values in April. However, in October conditions were reversed and in all but a single case, the osmotic values were higher in the coastal sagebrush association.

SUMMARY

1. The coastal chaparral and coastal sagebrush associations are represented in Santa Barbara County, California, the former being the more extensive. Sand dunes are found in limited areas along the coast.

2. Transpiration studies indicated that the water loss in the coastal sagebrush and coastal chaparral were approximately the same, with the dunes having about 14 per cent less than the coastal sagebrush association.

3. Osmotic values for practically all species were higher in the dunes than in the coastal sagebrush association in February and April.

4. The values for coastal chaparral species were practically all higher than were those in the coastal sagebrush in February and April; but in October conditions were reversed, nearly all values being higher in the coastal sagebrush.

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8 figs.

THE ECOLOGY OF SAY'S *LIMNAEUS ELODES*¹

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In 1821 (Journ. Acad. Nat. Sci., Philadelphia, Vol. 2, p. 169) the great naturalist, Thomas Say, described a large pond snail giving its habitat and locality as Canandaigua Lake. Indefiniteness of ecological station was characteristic of the early naturalists who deemed the name of the nearest town or body of water sufficient for location of a species. Such habitat names as Cayuga Lake, lakes Erie and Superior, Lake Champlain, and 'Lakes of Maine' are common in the older writings.

It is obvious that a pond- or swamp-inhabiting snail would not live in the waters of a large lake like Canandaigua and its exact ecological station must necessarily be sought in a normal habitat near the lake. No specimen of *elodes* has ever been found living in the lake. Many years ago the north end of the lake, where the outlet discharges its surplus waters, was an extensive swamp or marsh inhabited by *elodes* and other mollusks. This area has now been drained for building purposes. The southern end of the lake is also marshy. It is probable that the specimens from which Say drew up his original description came from the north end of the lake, either in the marshy tract bordering the outlet, or from a beach pool or pond bordering the upper end of the lake.

A few years ago, while exploring the east side of the lake, a large beach pond was discovered in which were living many large pond snails of the form known as *elodes*. These shells are exactly like Say's types deposited in the museum of the Philadelphia Academy and like his figures in the American Conchology. It is quite likely that the original shells came from a beach pond near the northern end of Canandaigua Lake, because the shores of both the west and a large part of the east side are very precipitous and do not afford space for beach pools of any description. The beach pond in question may therefore be taken as typical of the original locality.

This beach pond (fig. 1) is situated about three miles south of the City of Canandaigua on the east side of the lake, near a group of summer cottages erected on higher ground southward. The pool and the surrounding vegetation cover about five acres of which about three acres are included in the pool itself.

¹ Contribution from the Museum of Natural History, University of Illinois, No. 68.

VEGETATION

There are three characteristic zones of vegetation, (1) an outer belt of large forest trees; (2) a zone of bushes bordering the shore; and (3) a border of small water plants on the inner edge of the bushes.

The tree zone (fig. 1) consists of large trees, several specimens indicating an age of upward of 75 years. Seven species were observed as noted below: Hornbeam or blue beech (*Carpinus caroliniana* Walter), black ash (*Fraxinus nigra* Marshall), red maple (*Acer rubrum* Linn.), white elm (*Ulmus americana* Linn.), black oak (*Quercus borealis maxima* Eshe), hickory (*Carya alba* K. Koch), shell-bark hickory (*Cary ovata* K. Koch).



FIG. 1. Beach pond looking toward Canandaigua Lake. Buttonbush in center foreground. Open pool immediately in front.

The second (fig. 1) or bush zone consists almost exclusively of the Buttonbush (*Cephalanthus occidentalis* Linn.). Bordering this vegetation on the inner (pond) side, is the third zone, consisting of the following plants: Broad-leaved arrowhead (*Sagittaria latifolia* Willd.), pickerel-weed (*Pontederia cordata* Linn.).

The water area consists of a large pool in the center and on the south side in which the depth varies from two to four feet. Several bays of this pool extend into the bordering vegetation. The water plants in this pool consist of: Water-weed (*Elodea canadensis* Michx.), water milfoil (*Myriophyllum verticillatum* Linn.).

Insect life was fairly abundant in the pool and the following were specifically noted: Dragonfly larva (*Anax junius* (Drury) Selys), water boatmen (*Corixa* sp.), back-swimmer (*Notonecta undulata* Say), water scorpion

(*Ranatra* sp.), water bug (*Belostoma* sp.), water-strider (*Gerris buenoi* Kirk.), Whirligig beetle (*Gyrinus ventralis* Kirby), diving beetle (*Laccophilus maculosus* Germ.).

The holes of crayfish were observed but no specimens of this crustacean were seen. The list of animal life could doubtless be greatly extended by careful search carried on for this purpose, but no attempt was made to make more than casual observation of the life associated with *Mollusca*.

Limnaeus elodes, or *Stagnicola palustris elodes* as it now designated, was found abundantly in the pool, living on the muddy bottom which was filled with plant debris serving as food, or on the vegetation that lined the shore and filled the deeper water. Thirteen species and races of aquatic mollusks were associated with *elodes*, as noted below: *Sphaerium occidentale* Prime*, *Musculium securis* (Prime)*, *Pisidium roperi* Sterki*, *Valvata lewisi* Currer, *Helisoma pseudotrivolis* (F. C. Baker), *Menetus exacuous* (Say), *Menetus rubellus* (Sterki), *Gyraulus deflectus obliquus* (DeKay), *Gyraulus arcticus* ('Beck' Moller), *Gyraulus parvus* (Say), *Gyraulus circumstriatus* Walkeri (Vanatta), *Physa gyrina elliptica* Lea,² *Aplexa hypnorum* (Linn.).

Three land snails were also found on the shore and near the shallower parts of the pool: *Succinea retusa* Lea, *Succinea avara* Say, *Zonitoides nitidus* (Muller).

Several of the associations among the aquatic species appear to be unusual. *Valvata lewisi* has not been found, at least by the writer, in association with such species as *S. elodes*, *H. pseudotrivolis*, *Aplexa*, and other slough-inhabiting forms. With the exception of the species *Sphaerium occidentale*, *Helisoma pseudotrivolis*, *Aplexa hypnorum*, and *Stagnicola palustris elodes*, the molluscan fauna is one that might be found in a fairly large lake rather than in a comparatively small beach pool. The reason for this unusual association is probably that the small 'bay' which was cut off from the lake by the new beach or bar, was large enough and deep enough to provide a fairly normal habitat for such species as *Valvata lewisi* and the smaller Planorbids, at the same time providing more or less swampy or boggy habitats for such species as *Sphaerium occidentale*, *Helisoma pseudotrivolis* and *Aplexa hypnorum*.

CONCLUSIONS

The ecological environment of Say's *Limnaeus elodes* is such that it could not have lived in the waters of Canandaigua Lake, the general habitat given by Say. Its presence in a large beach pond or pool on the east side of the north end of the lake is evidence that the original habitat locality was of such a nature, and was situated either at the north end of the lake in the large cat-tail (*Typha*) area, now drained for building purposes, or along the shore of the northeastern part of the lake, the greater portion of the east and west

² The *Sphaeriidae* were determined by Dr. V. Sterki and the *Physa* by Mr. William J. Clench.

shores being precipitous and the lake waters deep. Specimens from the pool described, situated about three miles south of the City of Canandaigua, may be taken as topotypes. The species is now considered a geographic race of *palustris*, the common European pond snail. The American form is distributed from the Atlantic coast westward to the Rocky Mountains and from northern Canada southward to New Mexico. Several local races are known from the west and from the lake region of northern United States and Canada. Several of these are ecological races.

A COMPARISON OF TRANSPERSION RATES IN CHAPARRAL¹

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The scrub vegetation called chaparral has undergone such change from repeated fires, especially on the lower foothills of southern California, as to be termed "fire type" chaparral. This continued fire effect makes pertinent various questions of future management of this chief vegetative cover, questions whose importance is measured by the great economic value of the chaparral cover in water supply. The present investigation has to do with the relative rates at which eight common chaparral plants make use of the generally scanty soil moisture. The results indicate that certain of the species in question might well be favored, being rather conservative users of water.

CHAPARRAL

The chaparral area used in this investigation occupies a portion of the foothills of the Santa Monica Mountains lying to the north of the city of Los Angeles. The "fire type" chaparral covers the region extensively, occurring on a residual soil originating mainly from decomposing granite, the surface layer being dry, stony, and containing very little humus. It is mostly a shallow soil, with the granite frequently but a few inches below the surface. The rock is often of a crumbly nature. About fifty shrubs of the typical chaparral families and genera have been identified in the immediate region. Quadrat studies indicate a codominance of the chamise, *Adenostoma fasciculatum* H. & A., and the wild buckwheat, *Eriogonum fasciculatum* Benth. These two species possess narrow, linear, evergreen leaves, constituting exceptions to the general evergreen, broad-sclerophyll habit of the chaparral shrubs.

During the period of the investigation, September 29, 1930, to March 21, 1931, rainfall records in this immediate area showed a total precipitation of 9.78 inches, falling in the months of November, January, and February. The total for the entire rainy season of 1930-1931, October-May, was 14.17 inches. At the city of Los Angeles, nearby, the rainfall within the dates mentioned above totalled 8.96 inches, and the total for the entire rainy season of 1930-1931 was 12.50 inches. The average annual total at Los Angeles for 54 years is 14.95 inches. On this basis 96 per cent of the annual rainfall in this city has fallen within the seven months, October to April.

¹ The substance of this paper was presented before the Ecological Society of America at Pasadena, California, June, 1931.

During the collection of the data here presented the temperature in the chaparral varied from 12° to 32° C. Moderate winds usually prevail on these foothills of about 850 to 1100 feet elevation. The slopes vary from ten to thirty-five degrees and are cut by many ravines, thus affording a considerable variety in declivity and exposure.

It has been commonly observed that the root systems of chaparral shrubs are extensive in proportion to the aerial parts of the plant. The more superficial roots spread in all directions, and, besides these, there are generally deeply penetrating roots descending for considerable distances in rock crevices. The available soil moisture is limited. To determine which of the species are the lavish users of soil water and which are the conservative users is the main purpose of the present study.

Adenostema fasciculatum H. & A., chamise, *Ceanothus cuneatus* Nutt, buck-brush, *Penstemon spectabilis* Thurb., penstemon, *Quercus dumosa* Nutt, scrub oak, *Rhus integrifolia* B. & H., lemonade-berry, *Rhus laurina* Nutt, laurel sumac, *Salvia apiana* Jepson, white sage, and *Salvia mellifera* Greene, black sage, were studied as some of the more common plants of the southern California chaparral.

Penstemon spectabilis was purposely chosen for comparative purposes as a very probable lavish user of soil water. This species is about the lowest in growth habit, being, in this vicinity at least, a somewhat suffrutescent, perennial herb, one to three feet in height. The other species range from three feet in the sages to twelve or fifteen in the laurel sumac.

The anatomy of the leaves shows various structural arrangements for checking the loss of water by transpiration. *Rhus integrifolia*, *Ceanothus cuneatus*, and *Quercus dumosa* all have leaves which are rather heavily cutinized on the upper surface. *Rhus laurina*, *Salvia mellifera*, and *Adenostema fasciculatum* also have a cutin layer on the upper surface, but it is not so distinctive as in the other species. The leaves of *Salvia apiana* are characterized by hairiness on both surfaces with no cutin layer. *Penstemon spectabilis* has practically no cutin on either surface.

Although *Eriogonum fasciculatum* is one of the codominants of the area it was found to be impossible to utilize its leaves satisfactorily with the cobalt chloride paper method, because the small, linear leaves prevent the proper affixation of the paper. *Adenostema fasciculatum* has very similar leaves, but stump sprouts possess leaves of a somewhat different character, being of sufficient width to permit proper utilization of the cobalt chloride paper; leaves of this sort, therefore, were used exclusively with this species. On the stump sprouts of *A. fasciculatum* the leaves are flattened, the palisade and spongy cells short and rounded, giving the mesophyll a loose structure; stomata occur on both surfaces and possess an outer as well as an inner stomatal chamber.

The leaves of *Ceanothus cuneatus* have stomata mostly within depressions in the lower surfaces; the palisade is from six to eight layers deep, simulating

spongy tissue in the center of the leaf. Its leaves are considerably reduced in size.

Quercus dumosa has rather small leaves with many stomata on their lower surfaces, where the uncutinized cell walls are protuberant. Diminished leaves with curled edges occurring in this species are probably an adjustment to reduce water loss. Its palisade usually consists of two dense layers with a third below which is rather open. The spongy tissue is open and with the lowermost layer of palisade makes up about one-half of the mesophyll.

Rhus integrifolia, with leaves that are heavily cutinized on the upper surface and slightly less so on the lower, has both epidermal layers of compact, small cells whose walls are thickened on all sides. Its palisade tissue consists usually of a single compact layer, with sometimes a short second layer below. The spongy tissue is abundant but rather compact. Stomata occur only on the lower surface.

In *R. laurina* although stomata occur on both surfaces they are far more abundant on the lower; the palisade is two to three layers deep, and the spongy tissue is palisade-like, fairly open, and occupies about one-half of the mesophyll.

Salvia apiana leaves bear stomata on both surfaces and both are well covered with hairs; its palisade is about three layers thick, and the spongy tissue filling about one-half of the mesophyll, is rather dense, simulating palisade.

S. mellifera has a very wide upper epidermis, constituting about one-fourth of the total thickness of the leaves. Palisade and spongy tissues are prominent and about equal in amount. Stomata occur only on the lower surfaces of the leaves.

METHOD

A representative, mature individual of each of the eight different species was selected and used during the investigation, as serving best for the comparison of transpiration rates. Only mature leaves in healthy condition on these plants were tested. Because of the variation in transpiration rate of different regions of a given leaf, only that portion of a leaf blade situated approximately two-thirds of the way from the base of the blade to the leaf tip was employed. Both the upper and lower surfaces were tested on each occasion and the average of the two readings obtained.

The customary cobalt chloride paper method was employed (Bakke, '14, Livingston and Shreve, '16), using the Livingston sensitive blue paper with bright blue standard color paper for the initial and the pink standard for the final tone. All these papers were cut to the same circular size of eight millimeters in diameter, which is an area of a fraction over fifty square millimeters. The same piece of sensitive blue paper was not used more than two or three times and the pieces of the initial tone and final tone papers were changed for fresh ones after every few days of use. A stop-watch was employed to obtain the time intervals.

For determining the "index of transpiring power" the Harvey (Livingston, '13) appliance for obtaining the so-called free water surface reading of evaporation was used. The "relative transpiration index" was calculated by dividing the average transpiration rate for the two surfaces of the leaf by the reading from the moist blotting paper instrument.

A standard Centigrade thermometer, graduated in degrees, was read to obtain the prevailing temperatures. Readings of the evaporating power of the air were also made at five minute intervals from a porous cup atmometer mounted as directed by Johnson and Livingston ('16).

The days for the tests were selected so as to include such variations in the atmospheric conditions as sunny hazy, sunny clear, cloudy still, cloudy windy, and sunny windy days. The time variations included early morning, late morning, early afternoon, late afternoon, and evening hours.

Five hundred and seventy-one transpiration tests were made of the eight species during the experimental period. These readings, with those of the evaporating power of the air, evaporation over moist blotting paper, temperature, time of day, and rainfall were recorded in tabular form. From these tables representative charts were constructed for each day, with the particular variations of the day recorded. The "relative transpiration indices" for the entire experimental period were then calculated from the charts, and various conclusions drawn by means of inspection and comparison of the charted data (fig. 1).

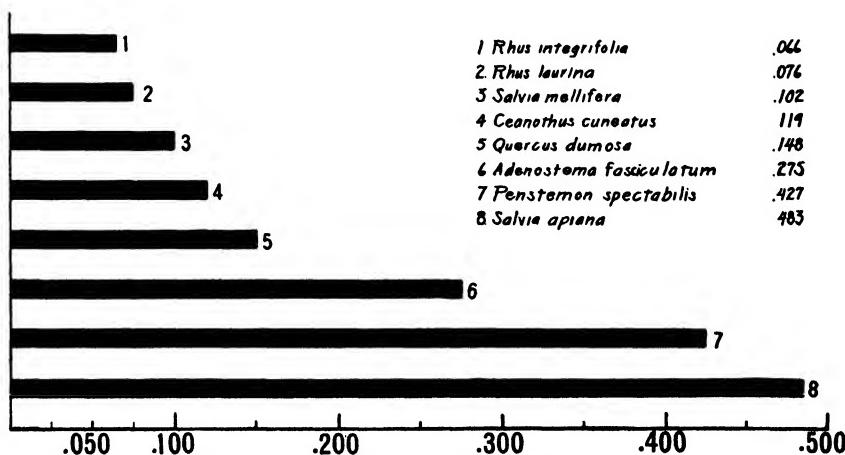


FIG. 1. Relative transpiration indices for eight species of chaparral plants.

RESULTS

The indices for *Rhus integrifolia* and *R. laurina* (.066 and .076) are somewhat higher than they should be. This is due to the fact that on certain days there were no changes in color of the blue cobalt chloride paper on the upper leaf surfaces for a period of over two hours. These readings could not be

included, therefore, in the determination of the "transpiration index" for the given day and consequently would not enter into the calculation of the grand transpiration index for the entire experimental period, which the above figures represent.

The time of day had a great influence on the transpiration rates. On sunny mornings between 10 and 11:30 loss of water by these plants was greatest, diminishing in the afternoon and becoming greatly reduced with the setting of the sun.

High transpiration rates were directly related to the high evaporation rates over the moist blotting paper, but not so directly related to the high rates of water loss through the porous cup atmometer, which seems to be influenced mostly by the temperature of the environment. In other words, the warmer the day the higher the rate of evaporation through the atmometer, but not necessarily so for the rate of water loss by the plant.

Direct sunlight seemed to have a retarding influence on the transpiration rates. On the whole the cooler the afternoon the higher were the transpiration rates.

Windy days had little effect on the transpiration rates of these plants, but did affect considerably the readings from the moist blotting paper instrument and from the atmometer.

Consideration of the structural arrangements that conserve water would place the first five species of the relative transpiration indices chart ahead of the remaining three in the series. But with the exception of *Rhus integrifolia*, which on structure alone would probably be ranked first or second, none of the other four could be placed in any way comparable to the series of the relative transpiration indices chart. In other words there seems to be nothing notable in the structure of these four species that particularly sets off one as being better able to conserve water than another.

The lower surfaces of the leaves transpired much more freely than the upper surfaces, in fact, in the case of *R. integrifolia* as much as twenty times faster.

Considerable cuticular transpiration was found in some of the species, especially in *Ceanothus cuneatus*, *Quercus dumosa*, and *Adenostema fasciculatum*.

Salvia apiana, with a thick covering of hairs on each surface of its leaf, is surprisingly the most lavish user of water of the eight species considered, exceeding even *Penstemon spectabilis* in this respect.

Tests comparing young and mature leaves of the same species indicated that the younger the leaf the more rapidly does it transpire.

SUMMARY

Of eight chaparral species tested by means of their relative transpiration indices *Rhus integrifolia* and *R. laurina* are indicated as highly conservative users of soil water. White sage, *Salvia apiana*, whose leaves bear a covering of hairs, appears to be the most lavish user of water.

With the possible exception of one of the sumacs, the general structural arrangement of the leaf appeared to furnish very little reliable information as to relative use of water.

The evaporating power of the air, temperature, and a few other environmental conditions, are shown in certain relations to transpiration.

Rainfall records indicate that the amount of soil water available to the plant may be the most influential factor in its rate of transpirational water loss.

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STUDIES OF POPULATIONS OF *PSEUDOCOCCUS BREVIPES* (CKL.) OCCURRING ON PINEAPPLE PLANTS¹

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The pineapple mealy bug, *Pseudococcus brevipes* (Ckl.) has been known in Hawaii primarily as a pest of pineapple fruit (Fullaway, '22, Illingworth, '26a) although one author (Larson, '10) considered the species in relation to pineapple rot. More recently the possibility of this species of mealy bug being concerned with the so-called "edge wilt" of pineapples has been considered. This consideration is a logical one since the observation that mealy bug infestation appears to start from the outer edge of pineapple fields has been commonly made and was referred to by Fullaway ('24). While the collapse of pineapple plants, particularly while in first ratoon, is obviously the result of a complex of factors, it is true that the typical case is one of dying back from the edges of fields, or from waste areas in the middle of large fields. No quantitative determinations of mealy bug populations appear to have been heretofore recorded but such studies have been conducted during the past year as a preliminary step to the evaluation of the effect of mealy bugs in contributing to edge wilt.² The results herein recorded present data on populations of mealy bugs encountered on planting material, the subsequent fate of these populations, the movement of mealy bugs into young plantings, and the status of these populations in fields up to twelve months old.

METHODS OF SAMPLING

Since pineapple fields are laid out in symmetrical blocks and the plants planted at measured intervals, samples may be taken at such intervals as to permit the whole sample taken to represent an average of the entire block. As large a number of plants has been taken as the limitations due to labor involved in care of the sample and the value of the plants would permit. These plants were pulled and placed in tight cloth bags. On returning to the laboratory these bags were fumigated over night. The plants were then dissected and the mealy bugs counted. Some limitations had to be placed on the forms counted since in the crawler stage the insect is under and around its parent in large numbers and adequate counting would have necessitated lifting each mature mealy bug in order to reach the crawlers still underneath. The standard

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² The careful assistance of Mr. K. Ito in connection with this study is gratefully acknowledged.

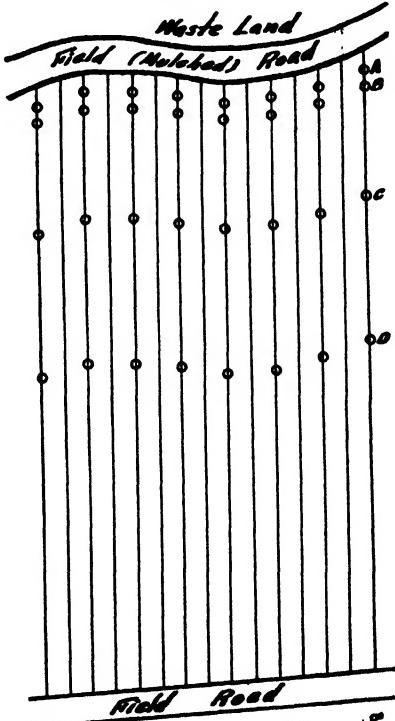
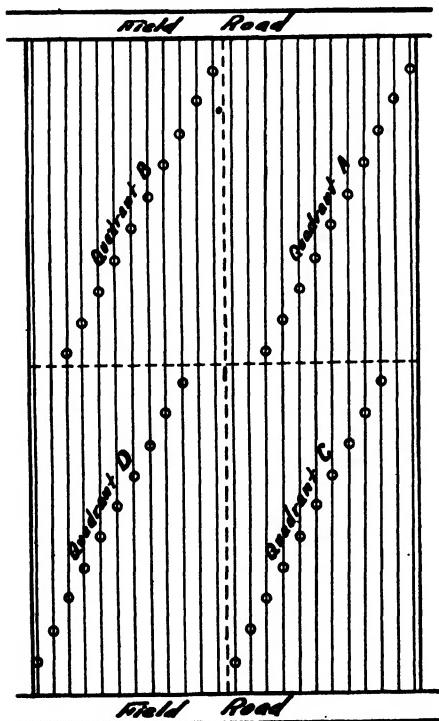
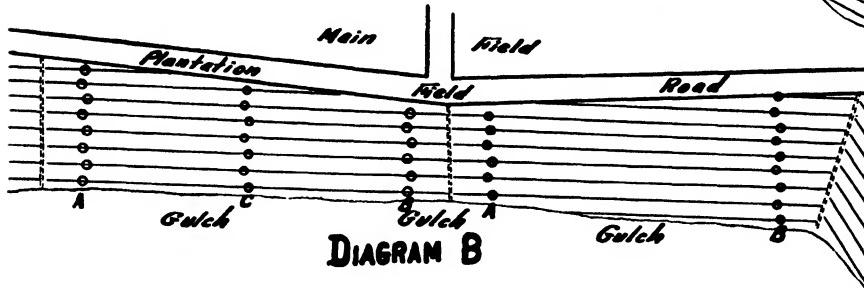
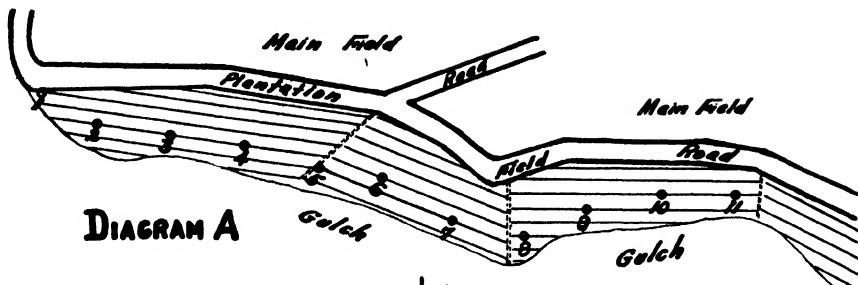


DIAGRAM A. Peripheral samples taken from a field bordered by a gulch.

DIAGRAM B. Samples at varying distances from the edge of a field bordered by a gulch.

DIAGRAM C. Samples from a regular rectangular plantation block.

DIAGRAM D. Samples from a block bounded on one side by wild vegetation.

adopted therefore was to count each bug which had established itself and had a waxy coating. A division was made in that mealy bugs found beneath the soil line on the plant were counted separately and classified as subterranean but the number of plants infested below the soil level was too small to justify recording in a separate column.

A number of plantation fields which were bordered by deep gulches were planted so as to include a small strip outside of the main plantation area on the upper edge of the gulch margin. These areas were planted for the specific purpose of studying the movement of mealy bugs and their control and much of the data of this study concerns these areas. Sampling in these cases consisted first of a peripheral sample since possibilities of infestation were considered as probably proportional to the amount of edge exposure. An example of this is seen in diagram A. The second plant in from the edge was taken every ten paces; the third plant in from the edge was taken every ten paces also but with the distances "staggered" as shown in the diagram. The portion of the plot sampled therefore was a strip around the periphery. Later, another type of sample was taken in these same plots when it became evident that the population of mealy bugs had established itself further inside the plot. In this case a strip was taken five paces from each end of each plot and plants pulled in a line as shown in diagram B. This type of sampling gave an indication as to how far within the plot the infestation had progressed.

Other experiments included regular rectangular plantation blocks. In this case samples were taken as in diagram C. Still other experiments included blocks which were bounded on one end by an irregular margin contiguous to wild vegetation. This type was sampled as in diagram D.

MEALY BUGS ON PLANTING MATERIAL

The mealy bug appears to prefer the most succulent tissue of the plant to be found. For a considerable period therefore, the greatest portion of the colony is in the soft tissue at or near the junction of the green tissue with the white. As the inflorescence appears there is a movement, first to the stem and then to the buds. Large masses of mealy bugs establish themselves on the fruit and later on the crowns and slips. These crowns and slips are used for planting material and, since in the summer of 1930 this material was found heavily infested with mealy bugs on one trimming ground, an opportunity was presented to study the course and ultimate fate of these populations. Sample A from trimming ground (table I) presents data obtained from crowns which were heavily infested with mealy bugs after being stacked, butt up, on a trimming ground for a month. The data include the effect of certain treatments which are not within the scope of this paper but are included to indicate the size of populations planted in the field as a result of the use of this planting material.

Comparison of populations on 29.VII.30 and 12.VIII.30 show rather definitely that reproduction can on occasion take place even on drying planting

TABLE I.—*Distribution of mealy bug populations*

	No. of plants	Per cent of plants infested	Average mealy bug population per plant
Sample A from trimming ground 29.VII.30.....	88	90	15
Untreated material from A			
At planting time, 12.VIII.30.....	86	100	114
15.X.30.....	52	86	8
11.XII.30.....	62	19	9
Treated material from A			
At planting time, 12.VIII.30.....	88	86	46
15.X.30.....	51	45	5
11.XII.30.....	22	9	11
Field 21, Helemano, Oahu. Planted 1.VI.30			
Check A			
20.XI.30 (diagram A).....	19	42	7
6.I.31 (diagram A).....	17	47	21
16.III.31 (diagram B).....	25	12	54
Check B			
20.XI.30.....	22	36	3
6.I.31.....	25	28	17
16.III.31.....	19	21	31
Check C			
20.XI.30.....	9	100	7
6.I.31.....	8	100	16
16.III.31.....	12	100	89
Check D			
20.XI.30.....	16	13	59
6.I.31.....	16	25	16
16.III.31.....	35	37	26
Check E			
20.XI.30.....	7	71	4
6.I.31.....	13	77	5
16.III.31.....	9	89	8
Check F			
20.XI.30.....	6	83	33
6.I.31.....	5	100	14
16.III.31.....	9	100	23
Field 22, Helemano, Oahu. Planted 1.VI.30			
Check A			
12.XI.30 (diagram A).....	24	92	29
7.I.31 (diagram A).....	21	95	31
9.III.31 (diagram B).....	17	59	36
Check B			
12.XI.30.....	11	100	97
7.I.31.....	10	100	83
9.III.31.....	27	81	23
Check C			
12.XI.30.....	17	88	64
7.I.31.....	16	88	30
9.III.31.....	14	79	44
Field 53-B, Kemoo, Oahu. Planted 1.XI.30			
Check A			
10.II.31 (diagram A).....	18	78	25
27.IV.31 (diagram B).....	18	56	30
Check B			
10.II.31.....	15	0	0
27.IV.31.....	14	0	0

TABLE I.—Continued

	No. of plants	Per cent of plants infested	Average mealy bug population per plant
Check C			
10.II.31.....	15	13	1
27.IV.31.....	16	19	28
Check D			
10.II.31.....	18	0	0
27.IV.31.....	11	0	0
Check E			
10.II.31.....	12	8	2
27.IV.31.....	12	0	0
Check F			
10.II.31.....	10	30	4
27.IV.31.....	15	27	9
Check G			
10.II.31.....	6	0	0
27.IV.31.....	7	0	0
Check H			
10.II.31.....	23	9	15
27.IV.31.....	20	5	1
Field K-1, Kipapa, Oahu. Planted 12.VIII.30. (diagram C)			
Quadrant A			
30.X.30.....	20	45	5
26.I.31.....	20	5	1
27.V.31.....	20	0	0
Quadrant B			
30.X.30.....	20	35	4
26.I.31.....	20	10	3
27.V.31.....	20	0	0
Quadrant C			
30.X.30.....	20	45	5
26.I.31.....	20	5	1
27.V.31.....	20	0	0
Quadrant D			
30.X.30.....	20	25	3
26.I.31.....	20	0	0
27.V.31.....	20	0	0
Field 22, Kahuku, Oahu. Planted 26.X.30. (diagram D)			
Line A			
28.XI.30.....	28	29	2
13.II.31.....	24	92	17
6.IV.31.....	28	93	37
Line B			
28.XI.30.....	28	32	4
13.II.31.....	24	79	21
6.IV.31.....	28	71	13
Line C			
28.XI.30.....	28	14	4
13.II.31.....	24	29	1
6.IV.31.....	28	7	1
Line D			
28.XI.30.....	28	7	5
13.II.31.....	24	25	5
6.IV.31.....	28	14	2

material. The enormous increase between these two dates was due to the appearance of large numbers of young which were able to establish themselves sufficiently to be counted, as described in the paragraph on sampling methods. A portion of this planting material was treated and the data show the population on this material. Immediately after the sample was taken the material was carted off and planted so that plots were available with two grades of initial infestation.

Samples taken on 15.X.30 and 11.XII.30 were somewhat smaller since these samples represented growing plants which would have to be replaced. The comparison, however, shows clearly enough that a heavy reduction in population had taken place after the two month interval. It may be of some significance that isolated populations of some size (*e.g.*, 15, 16 and 56 bugs per plant) could be found even after this interval but it is clear that the populations planted in the field on planting material do not, with rare exceptions, establish themselves. Data from four other experimental plots in widely separated localities are of the same type and lead to the same conclusion. Observations during the past year lead to certain hypotheses as to the reason for this failure. As has been stated above, the mealy-bug and ant constitute a biocoenose which normally, as will be seen later in this paper, is established at the edge of pineapple fields and continues, as time goes on, through the whole area. When a field has been properly prepared for planting, cultivation has been such as to break up and disperse *Pheidole megacephala* Fab. colonies so that mealy bugs planted within such an area are without the protection that ants normally afford. Another ant, the fire ant, also attends *P. brevipes* and the writer has one field under observation where mealy bugs had become established in the center of a newly planted field with this ant in attendance. It has been the experience of Libby, McNeill & Libby of Honolulu, Ltd., whose officers have done much experimental work on ants, that the fire ant, *Solenopsis germinata* Fab. var. *rufa* Forel, frequently has its nests deep in the ground and that normal cultivation fails to dislodge the colonies.

Another observation also tends to explain the disappearance of mealy bug colonies. It is the practice on pineapple plantations to replant at frequent intervals during the first few months after planting. Laborers pass down the rows, pulling out all those plants which have failed to grow or which show signs of being weak. New plants are then planted in the old planting holes. A large number of these plants were pulled out by the writer and his assistants and examined for mealy bugs and signs of mealy bug feeding. Practically all of these plants showed signs of mealy bug feeding on the new leaf tissue and scattered populations as high as 41 were found among them. The facts that of 557 plants examined only 7.7 per cent were infested with mealy bugs at the time and that many of the plants showed no signs of mealy bug feeding on the youngest one or two whorls of leaves indicate, as has been frequently observed, that mealy bugs will forsake a weak or dying plant. Since this was the third time that replanting had occurred in this plot it is evident that a good

many infested plants must have been removed. There are several species of Coccinellid beetles which are observed from time to time feeding on *brevipes* and these, no doubt, are contributory factors to the disappearance of mealy bug populations within the pineapple fields.

Isolated infestations of mealy bugs are found frequently enough in the middle of large fields, however, to indicate that, while the generalization that mealy bugs planted in fields with planting material disappear if *Pheidole megacephala* or *Solenopsis germinata* var. *rufa* are not in attendance is true, exceptions do occur and some of these introduced populations continue.

DATA ON POPULATIONS OF *PSEUDOCOCCUS BREVIPES* OCCURRING ON PINEAPPLE PLANTS

Peripheral samples: Fields 21, 22, and 53-B

The distribution of populations varies widely within a localized area and between areas. Field 21 (table I), sampled about 6 months after planting, showed an uneven distribution in the several sections of the plot. The maintenance of this variation for four months is seen from a comparison of the three samples. The third sample (16.III.31) indicates the general spread throughout some sections having heavy initial infestation. Outer edge infestation only is still marked in check A and noticeable in check D. Little change in size of populations was observable between samples 1 (20.XI.30) and 2 (6.I.31) but a general increase is noted in the third sample (16.III.31).

Field 22, Helemano (table I), of the same age as Field 21 and sampled first at approximately the same time, shows extremely heavy populations in the outer zones of the plot. The second sample (7.I.31) indicates the same percentage of infestation but some reduction in the size of infestations on individual plants even though two months had elapsed between samples. The third sample (9.III.31, diagram B) indicates that colonies had become established throughout the plot though populations over 100 appear only on the outer lines.

Field 53-B (table I) illustrates the variation in infestation and the continued freedom of most of the sections of this plot. The second sample (27.IV.31, diagram B) shows outer edge infestation still obtaining.

Samples from plantation blocks situated within a large pineapple field and without exposure to wild vegetation or old pine- apple fields: Field K-1, diagram C

A large sample of the planting material taken just prior to planting of this field revealed that 94 per cent of the plants were infested with an average population of 19 mealy bugs on the infested plants. Samples taken after planting are recorded in table I. The steady diminution in number of infested plants and in size of populations is additional proof of what already has been discussed in this paper in connection with mealy bugs on planting material.

Samples from plantation blocks bounded on one edge by an irregular margin contiguous to wild vegetation: Field 22, Kahuku, diagram D

A clear indication of a continued invasion from the outer edge in to the field is presented by the data.

To ascertain whether or not this concentration of population at the edge of the field held in the case of an older field a sample was taken in a 12-month-old planting bounded on one side by an old field which had been broken down and fallowed some time before the sample was taken. These data are in table II.

TABLE II. *Sample* taken to determine population in (approximately) 12-month old plantings with respect to proximity to old fallow area*

Field I, Kunia, Oahu

Sample 9.X.30

Plant No.	Mealy bugs	Plant No.	Mealy bugs	Plant No.	Mealy bugs	Plant No.	Mealy bugs
A— 5	I	A ₁ — 5		B— 5	7	B ₁ — 5	7
A 10		A ₁ 10		B 10	23	B ₁ 10	2
A 15		A ₁ 15		B 15	3	B ₁ 15	I
A 20		A ₁ 20	I	B 20	1	B ₁ 20	
A 25		A ₁ 25		B 25	1	B ₁ 25	
A 30		A ₁ 30		B 30	5	B ₁ 30	
A 35	I	A ₁ 35	20	B 35		B ₁ 35	2
A 40		A ₁ 40	I	B 40		B ₁ 40	I
A 45	6	A ₁ 45	I	B 45		B ₁ 45	I
A 50		A ₁ 50	87	B 50	4	B ₁ 50	
A 55		A ₁ 55		B 55	18	B ₁ 55	
A 60	47	A ₁ 60		B 60	22	B ₁ 60	26
A 65	I	A ₁ 65	I	B 65		B ₁ 65	I
A 70	90	A ₁ 70	8	B 70	2	B ₁ 70	
A 75	2	A ₁ 75	2	B 75		B ₁ 75	21
A 80	I2	A ₁ 80	32	B 80		B ₁ 80	
A 85	22	A ₁ 85	71	B 85	I	B ₁ 85	
A 90	47	A ₁ 90		B 90		B ₁ 90	
A 95		A ₁ 95		B 95		B ₁ 95	I4
A 100		A ₁ 100		B 100	2	B ₁ 100	I
A 120		A ₁ 120		B 120		B ₁ 120	
A 140		A ₁ 140		B 140		B ₁ 140	I
A 160		A ₁ 160		B 160		B ₁ 160	
A 180	2	A ₁ 180	I	B 180	8	B ₁ 180	6
A 200		A ₁ 200		B 200		B ₁ 200	
A 250		A ₁ 250		B 250		B ₁ 250	
A 300		A ₁ 300		B 300		B ₁ 300	

* Every 5th plant taken. Plant numbers indicate distance from old fallow area.

Though there is considerable scatter in these populations the general picture showing the heaviest population and plants infested grouped a short distance from the outer edge is clearly indicative of invasion from the old pineapple area.

TYPE OF EXPOSURE AND INFESTATION

Observation leads to the conclusion that the grasses are an important source of mealy bug infestation and fields contiguous to such hosts are liable to heavy infestation. There is a decided preference on the part of the mealy

bug for the most succulent growth available and young plantings made next to older fields are infested even though populations still continue on the older plants, although this may be a reaction on the part of the ants to a reduced secretion on the part of mealy bugs living on drying tissue. Mealy bug colonies have been observed to disappear from failing plants and populations are rarely found on plants in an advanced stage of wilt so that young plantings made next to ratoon fields are infested rapidly. Observation also indicates that populations are established more rapidly on young and succulent plants than on plants of the same age whose growth is retarded even though initial infestation occurred on the same day. Observation supports the conclusion that the principal factor in the movement of mealy bugs from wild hosts and older pineapple fields to contiguous new plantings is the ant *Pheidole megacephala* Fab. although several other species have been recorded from time to time as attending mealy bug colonies (Illingworth, '26).

SUMMARY

The pineapple mealy bug (*Pseudococcus brevipes* Ckl.) becomes established on planting material while this material is still attached to the mother plant. The species persists on this material while it is drying on the trimming ground and on occasion the mealy bug can reproduce under these circumstances so that large populations of mealy bugs may be planted in new fields along with the plants. Most of these populations disappear, either as the result of failure of ants to become established in the same areas quickly enough, or by the action of predators, or by the replanting process which eliminated retarded or sickly plants. Occasional plants remain infested, however.

After the field is planted infestation occurs first on the outer edge and moves in gradually. There is some evidence that the rate of movement is influenced by the size of initial populations. In new fields bordered by wild vegetation or by old pineapple plantings, infestation is extremely variable both as to time and size even within localized areas, but in some cases results in high populations being established within six months after planting. This variability in infestation sometimes persists over a long period of time. The big-headed ant, *Pheidole megacephala* Fab., is the principal factor in mealy bug movements from wild hosts and old pineapple fields into new plantings.

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REVIEWS

A VEGETATION MAP¹

Although much has been written on the flora of the Alps, and indeed on the same area covered in this treatment, the present work has a new point of view, emphasizing chiefly the historical changes. The elaborate map, on a scale of 1/50000 and roughly 16 × 24 inches, shows in detail the distribution of vegetation in the upper Reuss Valley lying just north of the St. Gothard Tunnel in Switzerland. The utmost has been done to preserve clarity; though six colors as well as many symbols are employed, the work has been done in a pleasing manner without obscuring the underlying contours and place names, and it is intended as a model in its field. The legends are concise and easy to interpret. Above the timber line the area of vegetation (the *Carex curvula* zone), in conformity with proposed international scales, is colored red.

The dominant note in the accompanying text is the human influence on the vegetation. In elaboration of this theme man is traced from the Stone Ages through the Roman period to the permanent settlement of the upper valley, which began in the middle of the thirteenth century when the St. Gothard Pass was first utilized. From this time on the forest lands have suffered greatly from grazing, cutting and burning, so that practically no forest remains in its primeval state. The problem of treating the vegetation is thus a difficult one, and it is solved by introducing graphs showing the percentage of various ecologic groups of introduced plants in each zone. Beginning at the lowest altitude the five recognized zones are the *Quercus sessiliflora-Tilia cordata*, the beech, the fir, the *Carex-Pinus cembra*, and the *Carex curvula-Vaccinium-Loeselcuria*. Treatment of each of these zones includes notes on the component plant associations, and what is of greater interest, the listing of individual species according to their geographical affinities. For example in the beech zone 40 per cent of the species are *eurasiatic* and *eurosiberian*, 8 per cent are *middle-* and *south-European*, 14 per cent are circumpolar. The geologic, edaphic, and climatic conditions are discussed, sometimes illustrated by sketches, and as is to be expected in a modern work on plant geography, there are numerous references to the last glaciation, to relict species, and to pollen-analysis of bogs. Even without much knowledge of German the map and its text should afford one a good view of plant associations in the Alps.

¹ Schmid, Emil. 1930. Vegetationskarte der oberen Reusstälern. *Beit. Geobot. Landesf. Schweiz*, 16: 64 pp., 7 figs., 2 pls., 1 colored map. Hans Huber, Berlin. 9.50 Fr. (Swiss).

and there is an instinctive wish to see similar maps constructed for mountain valleys in America.

H. K. SVENSON

BROOKLYN BOTANIC GARDEN

ANIMAL AGGREGATIONS¹

The various harmful effects of overcrowding among animals are well known; but the physiological disadvantages of what may be termed "under-crowding" are less familiar and, at first sight, somewhat unexpected. Most biologists will, however, be acquainted with Pearl and Parker's demonstration that sparse populations of *Drosophila* grow less successfully than denser ones, although still higher concentrations again produce harmful effects; and with the experimental studies of Professor Allee himself upon the beneficial influences of crowding among isopods and other animals. The author's main thesis that the physiological disadvantages of undercrowding form the basis of various types of aggregations in lower animals which can scarcely be termed social, yet may form the starting point for the evolution of higher social groupings, appears to be well supported by the evidence he has collected.

It is difficult to do justice to this book in a short review. It is such a very good book, covering a remarkably wide field of scientific literature in a manner marked both by critical insight and breadth of view. The author modestly calls it "notes on an unsolved problem." In fact he has skilfully gathered together the threads of a vast subject whose future development can scarcely be foreseen.

The early part of the book deals, among other things, with a modified form of Deegener's classification of aggregations. As to the value of such systems of terminology opinions differ. "Penny plain; twopence coloured; pay your money and take your choice." Here the reader encounters a positive riot of strange terms which hardly justify the extra two cents and which will make him glad or sorry according to his disposition. Is it necessary for a student to learn to call a family a "patrogynopaedium"? At any rate a mild protest seems justifiable, if not in the name of science, then in the name of ancient Athens.

Certain theoretical points require clarification and should be brought into relation with other phases of work on animal population. For instance, what do we mean exactly by the words "harmful" and "beneficial" in relation to density of numbers? The mere capacity to live at a high density without direct physiological harm and without lowered rate of increase, is not beneficial unless it agrees also with the ecological criteria of optimum density (*e.g.*, not over-eating food supply, not giving rise to epidemics, etc.). No factor affecting density of numbers is in itself harmful or beneficial without reference to the rest of the environment. Thus flocking for protection may well lead to

¹ Allee, W. C. 1931. *Animal Aggregations, A Study in General Sociology*. University of Chicago Press, pp. i-viii, 1-431.

greater mortality from disease. And after all this is said, the only ultimate criterion of biological success is whether evolution takes place rapidly over long periods without extinction. Since we do not yet even know under what ecological conditions of population (high density, fluctuations, etc.) such "success" is attained, the use of such terms as "beneficial" should be made with care when they are applied to numbers.

These are some of the points which are suggested by reading Professor Allee's book, which invites discussion and should be read by every biologist.

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POSTGLACIAL FORESTS OF ITALY

The investigations of postglacial climate and vegetation which have been so extensively carried forward in northern Europe have now been extended to Italy.¹ Keller has made pollen analyses of many of the bogs of the Piedmont, Lombardy and Venetia Provinces of northern Italy. He seems particularly fitted to this task on account of the similar studies he has conducted in the Swiss bogs with which he makes numerous comparisons. The results show expected similarities with those from more northern deposits.

Following the retreat of the last ice sheet the forests seem to have been similar to those of central Europe, dominated by *Betula*, *Salix*, and *Pinus*. This period known as the Birch Period, possessed a cool climate and was followed by a slightly warmer Pine Period with forests dominated by *Pinus*. During this period *Picea* and *Abies* appeared, the former migrating from the east and the latter from the west. Unlike the postglacial forest histories of Scandinavia, Germany and Switzerland, the Pine Period in northern Italy was not succeeded by a *Corylus* Period. Although *Corylus* was present in northern Italy, it only reached a maximum of 37 per cent in contrast with 157 per cent in northern Switzerland and 200 per cent in northern Europe. This was followed by a forest of *Quercus*, *Tilia* and *Ulmus* (Oak-mixed forest Period). It is interesting to note in connection with the latter period that a warmer climate than the present one prevailed in northern Italy. This was shown by Andersson, in his *Beitrage zur Kenntnis des spätquartären Klimas Norditaliens. In Postglaziale Klimaänderungen, Stockholm. 1910.*, who based his conclusions on a study of macroscopic plant remains found in the oak-mixed horizon. He found remains of *Vitis vinifera* and *Trapa natans*, both of which now have a more southern limit.

After this there seems to have been a gradual cooling of the climate marked by the development of forests dominated by *Fagus*, in the Beech Period, followed finally by *Castanea* and the forests of the present day.

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¹ Keller, Paul. 1931. Die postglaziale Entwicklungsgeschichte der Wälder von Norditalien. *Veröffen. Geobot. Institut. Rübel in Zürich*, 9: 1-187.

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NOTES AND COMMENT

BIOCLIMATOGRAPH, AN IMPROVED METHOD FOR ANALYZING BIOCLIMATIC RELATIONS OF INSECTS

Ball-Taylor's climatograph¹ has now become a recognized standard method for analyzing the relations of insects to the climate of a given region, or of a season (see Tehon, '28; Cook, '31; Uvarov, '31). There is no doubt that the method presents considerable advantages when a comparison of two, or more, climates must be made in order to ascertain their respective influences on an insect, and to deduce from the results which climatic features are of controlling value. The actual comparison is made between the polygons representing the climates and the differences, or similarities, noticed are then discussed from the point of view of their probable importance in the life-history of the insect.

Thus, in the ordinary climatograph, the life history of the insect is not represented at all, while it would obviously facilitate the comparison of the graphs, if they served to illustrate the climate in its relation to the life-history. This can be attained by a simple modification of the ordinary climatograph, namely, by using the lines connecting the monthly points to denote the stages, in which the interval is passed by the insect. If, for example, the hibernation occurs in the egg-stage, the lines connecting the winter months should be dotted; a broken line should connect the months in which the larval stage occurs; etc. A glance at a *bioclimatograph*, as a graph of this kind may be called, would show at once the climatic relations of the insect in the particular region, or in a particular season, and a comparison between two climatic environments *in their relation to the life history* of the insect becomes very easy.

The following example, based on the author's field studies on the Moroccan locust (*Dociostaurus maroccanus* Thunb.) in Asia Minor in 1931² is offered to demonstrate the possible use of bioclimatographs.

The central parts of the peninsula of Asia Minor are occupied by a high plateau, which in the west slopes down to the sea-level. During great outbreaks of locusts the whole western part of the peninsula, comprising the slopes and the littoral plains, as well as fertile river valleys, is invaded by locust swarms. However, during the years when locusts are in the minimum, *i.e.*, not swarming, they concentrate mainly in a very definite zone of the upper slopes, about 700–800 meters above the sea-level. A comparison of the climate of these reservations, as they are called, and of the invasion zones is of interest as it may help to elucidate the factors which in the normal years favor the locusts in the reservations, and control them in the invasion areas.

The two bioclimatographs are shown on the figure (fig. 1). The top graph is that for reservations, the bottom one for the plains. The life-cycle of the locust in reservations includes a very prolonged egg-stage, lasting from the middle of July throughout the summer, autumn and winter months, until the end of April when the hatching of larvae takes place. The larval development lasts till about June, and this month and the first half of July are passed in the adult stage. The enormously extended egg-stage is obviously due to the lack of moisture during the summer and early autumn, the eggs being then in a quiescent state; later in autumn, rains begin, but the temperature soon falls below the effective degree, and a quiescence due to cold follows until spring.

¹ The commonly used expression "climograph" is an unnecessarily corrupted version of "climatograph."

² A full report on these studies will be published elsewhere.

In the plains, the climatic conditions are very different from those in the reservations, and the average life cycle of the locust is also somewhat different, generally speaking. The hatching of larvae occurs there earlier than in the hills, about the middle of March, and the beginning of other stages is advanced accordingly.

A direct comparison of the two bioclimatographs shows that the greatest climatic differences are observed during the winter months, which are passed in the egg-stage. Still more obvious become the differences if the following graphical method of comparison is applied. Since the conditions in reservations are presumably very favorable, a rectangle, two sides of which represent the maximum and the minimum monthly precipitation, and the two others the maximum and the minimum mean monthly temperature,

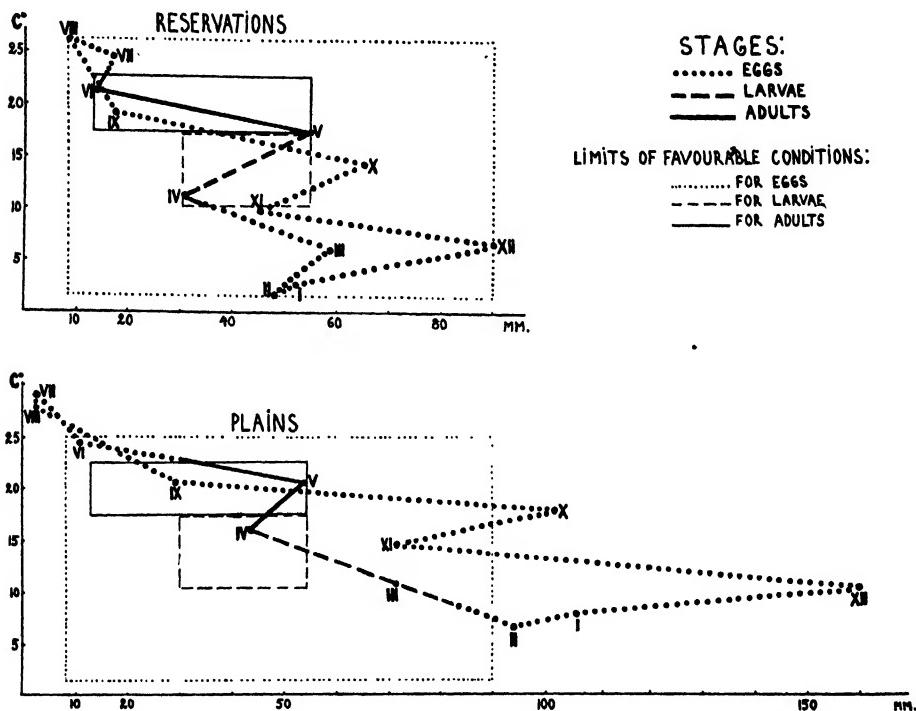


FIG. 1. Bioclimatographs representing the life history of the Moroccan locust in relation to climate in two stations.

would represent the range of the two climatic factors acting on eggs in the reservations. This *rectangle of favorable conditions* for eggs is shown on the figure by thin dotted lines, so that its relation to eggs is clear. If we now superimpose this rectangle on to the graph for the plains, it becomes at once obvious, in which months the local climatic conditions are unfavorable for eggs. We see, namely, that the graph for eggs projects beyond the rectangle during July, August and a part of September, but this deviation is very small and scarcely of controlling value. On the other hand, there is a striking deviation from favorable conditions observed during the winter months. This suggests the possibility that the winter conditions are the controlling factors in the plains, as far as the eggs are concerned. Indeed it is known that eggs of the Moroccan locust can be forced to develop at any time of the year if kept moist and at a sufficiently high temperature. The abundant precipitation and high temperatures of winter months in the plains

must cause a premature development of the eggs, and the larvae hatched in winter have little chance of survival.

A rectangle of favorable conditions for larvae (thin broken line), when transferred to the graph for plains, does not cover the larval portion of this graph. It appears that larvae in the plains are exposed to a much greater degree of moisture than in the reservations, while the temperature conditions remain favorable. Thus, excessive rainfall in spring may constitute another controlling factor acting on larvae.

The conditions to which adults are exposed in both areas do not differ substantially, the adult graph in the plains being almost entirely included within the rectangle of favorable conditions for this stage (thin continuous line).

The above example should make clear the principle of bioclimatographs, and the rectangle method for their comparison. The advantages of this type of graph are obvious, since it permits a rapid graphic comparison of local environments in relation to life history. Of course, the comparison merely reveals the *probable* controlling factors, and their effectiveness should be checked by suitable physiological studies on the respective stages of the insect, but this is a general consideration applicable to all climatographic studies.

It is easy to see that bioclimatographs can be adapted to various types of life-cycles of insects, though they are more suitable for studying those with one annual generation. The conventional signs can be multiplied when necessary. For example, it would be easy to introduce special signs to differentiate an active larva from a dormant one, etc.

The attention of those attempting to use bioclimatographs must be drawn to the fact, which may be easily overlooked, that the point for a particular month represents the mean temperature and the total amount of precipitation for the month. Therefore, the line connecting, for instance, the points for May and June should be regarded as representing the course of the two meteorological factors during June. This is, of course, not quite correct, but when necessary and possible the graph can be made not for whole months but for five or ten day periods, and this would render it more exact. This procedure would be probably particularly useful in the case of insects producing several generations in a year.

There is scarcely any need to add that bioclimatographs can be based on combinations of any climatic factors, just as the usual climatographs (see Tehon, '28).

The method is offered here only as a suggestion, in the hope that it will be tested by ecologists, with a view to improving or modifying it.

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PREMATURE GERMINATION OF FOREST TREE SEED DURING NATURAL STORAGE IN DUFF

For some years forest investigators in the Pacific Northwest have been aware of the considerable quantity of tree seed which accumulates in the duff of heavy virgin timber stands and apparently retains its vitality for a few years in a sort of natural cold-storage condition. The major portion of the luxuriant regeneration which frequently follows logging and forest fires in the western white pine forest of northern Idaho has, in fact, been attributed by many foresters to this stored seed. The theory is that wholesale

germination is stimulated by removal of the dense overwood shade and consequent raising of temperature of the cold and damp storage medium.

The amount of viable seed in the duff in relation to the time elapsed since the last seed crop has, however, never been accurately determined. As an answer to this question is essential to any proper understanding of the rôle played by stored seed in the regeneration of burned and cutover areas, the Northern Rocky Mountain Forest Experiment Station has been conducting a series of tests in which seed is stored under natural conditions for periods up to eight years in length to see how long and how much seed will remain viable.

One very interesting fact brought out to date by recent storage experiments is that a certain amount of stored seed is lost by premature germination. For some unknown reason, some seed germinates preceding any disturbance or opening up of the overwood canopy. The accompanying photograph, figure 1, shows seed that germinated under the

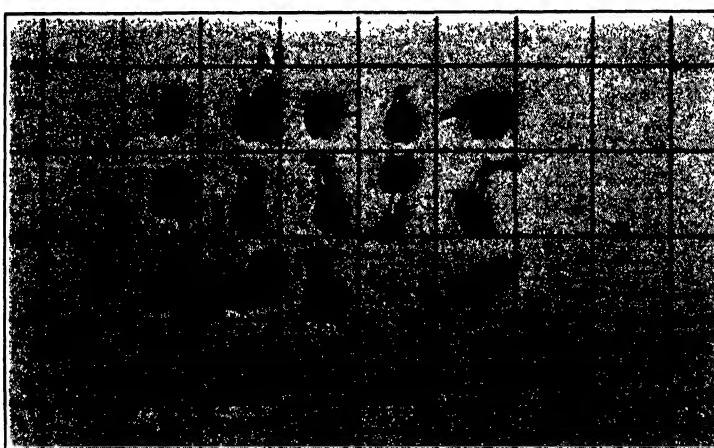


FIG. 1. Seed of *Pinus monticola* germinating during the second year of storage in duff under a stand of virgin timber.

dense shade of an overmature mixed stand of western white pine, *Pinus monticola*, western hemlock, *Tsuga heterophylla*, lowland white fir, *Abies grandis*, Douglas fir, *Pseudotsuga taxifolia*, and western larch, *Larix occidentalis*, during two years of storage in the raw humus characteristic of such stands. Most of this germination took place during the second season of storage, less than one per cent germinating in this manner during the first season. As the resulting seedlings promptly died, due to unfavorable light and moisture conditions created by the presence of the overwood stand, seeds germinating in this manner are wasted as far as future regeneration of the area is concerned. As about one-third of the viable seed originally stored in the tests described has germinated and died in this manner in the first two years of storage, it is evident that this premature germination is one of the factors which determine how long and how much of the seed of any one crop of western pine cones will remain dormant in the duff until the removal of the overwood stand and hence be available in regenerating the area.

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BRITISH ECOLOGICAL SOCIETY TO PUBLISH JOURNAL OF ANIMAL ECOLOGY¹

The British Ecological Society has decided to go ahead with its project for the publication of the Journal of Animal Ecology, and the first number will probably appear in May, 1932. The Editor will be Charles Elton of the University Museum, Oxford, and the Assistant Editor will be A. D. Middleton, who is associated with Elton at the same museum. Elton is well known for his "Animal Ecology,"² his "Animal Ecology and Evolution,"³ and a good many articles. Middleton has contributed papers to the British Journal of Ecology and other periodicals. Under such editorship, the new journal is certain to be scholarly and its reviews and notices to be accurate and comprehensive.

The Journal of Ecology has lacked space for the increasing number of papers dealing with animals which have been submitted. Various practical difficulties prevent the expansion of the Journal of Ecology to include these papers. At present they are published in a large number of British journals, as is evident from the abstracts in the Journal of Ecology. Incidentally, the collection of these abstracts is a laborious task for which the future Editor of the Journal of Animal Ecology deserves great credit.

The Council of the British Ecological Society decided that steps ought to be taken now for centralizing to some extent these widely scattered papers on animal ecology, and also, by planning, to anticipate the future development of the subject. At present there is a risk that the subject will become split into isolated compartments attached to special scientific and economic spheres. Already in America a great deal of ecological work, both on animals and plants, is done in various more or less separate fields. One has but to look at Biological Abstracts to be impressed with the vast amount of literature containing interesting ecological results but classified under other headings. The probable reason is that the ecological viewpoint has spread out into other fields.

The Journal of Animal Ecology will be under the control of the British Ecological Society, but separately financed and edited. It will contain papers dealing exclusively with animals, such as studies on population, migration, and allied problems. Papers covering comprehensive biological surveys including both plants and animals, papers on biotic communities, and such problems as the effects of grazing on plant succession, will continue to appear in the Journal of Ecology. The new journal is intended as an organ of research on animal ecology in the British Isles, though of course the results and principles established will have a much wider application. Eventually also, one would expect it to include papers on animal ecology outside of Great Britain. It will dovetail with the Journal of Ecology, which will continue to be the forum for discussion of general ecological theories.

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¹ Two issues per annum beginning May, 1932. Obtainable from the Cambridge University Press, Fetter Lane, London, E. C. 4, at 30 shillings (\$7.50 at par) or 25 shillings for members of the British Ecological Society.

² Elton, Charles. 1927. *Animal Ecology*. London, Sidgwick and Jackson, Ltd.

³ Elton, Charles. 1930. *Animal Ecology and Evolution*. Oxford U. Press.

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FACTORS INFLUENCING WILD LIFE IN CALIFORNIA, PAST AND PRESENT¹

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ORIGINAL CONDITIONS

In order properly to indicate the ecologic factors affecting wild life which are and have been operative in California, it will be necessary briefly to indicate the conditions which existed before American occupation. No adequate descriptive account of the native animal life and its ecologic relations is available for that period, but by taking fragments from the accounts of early travellers and by projecting backward knowledge gained after 1850, some appreciation of the original conditions may be had.

All early accounts agree as to the abundance of wild life. To mention only a few conspicuous species, the plains of the Great Valley were inhabited by tule elk, American antelope, grizzly bears, coyotes, ground squirrels and jack-rabbits; beaver were numerous in the streams; and water fowl abounded during the winter months. The foothills were populated by black-tailed and mule deer and valley quail; Roosevelt elk and black-tailed deer were present in the humid coast belt, while antelope, sage-hen and jack-rabbits tenanted the Great Basin. The deserts were populated mostly by small species.

REDUCTIONS IN ANIMAL POPULATIONS

From this variety and abundance of wild species, the Indians, relatively sparse in numbers by comparison with the present-day population (Indians in 1834, 260,000 [Merriam, '05, p. 598] or 133,000 [Kroeber, '25, p. 882]; present inhabitants of California 5,677,251, by census of 1930) took limited toll since their weapons and traps were relatively crude and they depended extensively upon vegetable foods for subsistence. But the white explorers, travelers, and immigrants from the first exploited the native wild life for food and fur. Elk and antelope were reduced rapidly; grizzly bears were

¹ Presented in the symposium on "Ecologic Aspects of Wild Life Management" at the New Orleans meetings. Contribution from the Division of Zoology, College of Agriculture, University of California.

killed in numbers, the fur-bearing species were trapped so extensively that their numbers greatly diminished. Ducks, geese, quail and other birds suitable for food were shot in enormous numbers and even in the latter decades of the nineteenth century became noticeably reduced. The process thus initiated over 80 years ago has gone on with only limited restriction until now but scattered remnants of elk, antelope and sage-hen remain, grizzlies are represented, if at all, by a few isolated individuals, quail, doves, waterfowl, and fur-bearers continue at a small fraction of the original numbers, and possibly only deer remain in something of their original abundance. Mountain lions, coyotes, wild-cats, jack-rabbits and ground squirrels have been systematically reduced by specific "control" agencies.

ECOLOGIC PROVINCES OF CALIFORNIA

The major ecologic provinces of California include (1) the floor of the great central Sacramento-San Joaquin Valley, the Los Angeles plain and numerous smaller valleys and connectant flood plain areas, (2) the southeastern deserts, (3) the foothill chaparral and scrub-forest, (4) the montane forests of the Sierra-Cascade system, of intermittent distribution to the south, and on certain inner coast ranges, but practically continuous on most of the Sierra Nevada, (5) the northwestern humid coast redwood belt, and (6), the great basin sagebrush plateau in the northern and especially eastern portion of the state.

The lowland valleys are traversed by numerous streams which primitively were bordered by extensive swamps and overflow areas developed especially during winter floods. A number of large lakes (Buena Vista, Tulare, Honey, Eagle, Goose, Rhett, and Lower Klamath) of fluctuating character existed, bordered by extensive marshes.

MODIFICATIONS BY MAN

Modification of the original conditions by various human "developments" consist in essence of the following:

Agriculture

1. The planting of cereal and field crops, vineyards and orchards, on open areas previously covered chiefly by grasses and herbs on lowland plains and flat valley floors or low hills.
2. The clearing of foothill and lower mountain slopes of chaparral or forest cover and replacing with vines or orchards.
3. The grazing of domestic livestock on plains and upland areas, often to the point of severe depletion of both native and introduced grasses and herbs and also possibly with depletion of the mineral supply in the upland areas.
4. The husbanding of water by accumulation in reservoirs to be distributed to cultivated areas as needed; accumulation of water for hydro-electric

power, with or without subsequent use in irrigation; pumping out of accumulated subsurface water supplies with consequent lowering of water table; decreased lowland stream flow (often complete cessation) with lesser amount of lowland flooding in winter and reduced subsoil irrigation during the remainder of the year.

5. The draining of lakes or marsh lands; reclamation of lowland deltas, stream margins, and overflow areas, by levees and dikes; straightening of major stream courses to effect more rapid runoff during winter flood periods, resulting in a lessened lowland stream flow in the summer season.
6. The "reclamation" of arid or semi-arid areas by importing water from distant hill or mountain regions.
7. The reduction of carnivorous mammals and birds likely to prey upon domestic livestock, and of rodents and of spermophilous or frugivorous birds likely to feed upon crops.

Lumbering and Forestry

1. The removal of the tree cover in coast ranges and the Sierras and the burning of chaparral and slash, resulting in alteration of the vegetational climax or initiation of a new cycle of plant succession over large areas, and, locally, of increased erosion.
2. The restriction of burning in forests, and especially in chaparral areas, leading in some instances to replacement of grassland by chaparral and possibly also leading to alteration of the soil mineral relations.

Mining

Hydraulic mining formerly disturbed foothill and lower mountain stream beds and marginal areas, allowing increased opportunity for erosion and increased accumulation of fine detritus which in periods of heavy rainfall washed down major stream courses in large amounts resulting in the elevation of lowland river beds, the increased flooding of adjacent areas, and altering the character of marshlands in the San Francisco Bay region.

Industrial development

Smelter fumes locally have caused reduction of the vegetation in circumscribed areas; stamp mills have increased the amounts of fine débris in streams locally; petroleum wells and the shipment and refining of oil have released local accumulations of oil which have covered some waste lands. Pumping out of oil-contaminated water ballast by oil tankers approaching the coast formerly released large amounts of oil on ocean beaches and adjacent waters, but this is now largely abated. Factory and sewage wastes still constitute a very minor factor in water pollution in California.

Human settlement and agricultural development is concentrated in the lowland areas, more specifically in provinces 1 and 3. Crop production with

tillage has occupied the flat lands of these areas and even up to fairly steep slopes in provinces 3, 5, and the margin of 4. Grazing is, and has been, practiced in all suitable areas of the state from the earliest times. Water relations have been changed importantly in provinces 1 and 3, and locally elsewhere. Lumbering has been important in provinces 4 and 5. The relative importance of these factors in the various provinces of the state is suggested in the accompanying table.

Relative effects² of various human activities in California during the "American" period

	Settle- ment	Agricul- ture	Change in water relations	Grazing	Deforest- ation
1. Lowland valleys and plains . . .	xxx	xxx	xxx	xx	
2. Southeastern deserts	x	x	x	x	
3. Foothill chaparral	x	xx	xx	xx	xx
4. Montane forests		x		xxx	xx
5. Northwest humid coast belt . .	x	xx	x	xx	xxx
6. Northeastern plateau		x	xx	xxx	x

² Degree of change of original conditions is indicated by number of crosses (e.g., x = slight).

SUPERVISION AND "CONTROL" OF WILD LIFE

Human supervision of the wild life of California dates from the period immediately following the gold rush. In 1852 the first game law was enacted giving protection to certain species. Since that year efforts at protection, supervision, and encouragement have been practically continuous and have become increasingly complex.

Efforts at managing wild life all reduce to the following basic principles.

A. Control of activities of the human population in relation to wild life:

1. Closed seasons to afford species protection during breeding season or longer periods.
2. Bag limits to restrict total levy upon wild populations.
3. Supervision or elimination of commercial capture and sale.
4. Limitation on the manner of take, type of weapons, nets, etc.
5. Districting to make seasons for capture appropriate to condition of animals in different biological provinces.
6. Prohibition of capture on certain areas, or for certain species greatly depleted or generally rare.
7. Restriction of water pollution and providing artificial fish-ladders over man-made stream barriers.

B. Direct efforts in respect to wild life itself:

1. Investigation to determine the biological basis for appropriate administration.
2. Gathering of data on kinds and amounts of wild species captured in the effort to anticipate depletion, especially with respect to commercial use.

3. Killing of certain predatory species in the effort to release pressure on the more desirable species.
4. Efforts to control species damaging agricultural crops by poison baits, gassing, hunting, trapping, or fencing with or without alteration in numbers of other species.
5. Planting of food crops.
6. Propagation and distribution of the young or adults of native or alien species to replenish, supplement, or supplant the existing wild stocks of native species.
7. Establishment of breeding, feeding and resting areas (refuges).

Obviously all of the efforts under heading "A" are or should be planned with respect to the life history requirements of the various species involved. Perhaps the only factors of ecologic importance in the control of human activities in California are in groups 5 and 7. Supervision is exercised over gun clubs, both "commercial" and private, which have properties especially developed to attract ducks and geese. As the amount of natural marsh land has become reduced through agricultural and other reclamation activities there has been intensive development of artificial marshes and ponds which are carefully managed and baited with grains to attract the more desirable ducks. The balance between the natural marshes and the artificial or "controlled" marshes has now swung so far that the latter are of great importance, especially during periods of drought and of scanty autumn rainfall, because the ducks are concentrated on club ponds; in fact, there is now very little satisfactory duck shooting on freshwater anywhere in California save at gun clubs. Proper management of the clubs is, therefore, of paramount importance in respect to future supply. The curtailed open season of one month in 1931 was opposed by organized duck hunters in California on the ground that with only 8 or 9 days (Wednesdays and Sundays) of shooting per year, many clubs would be abandoned, and with their abandonment still further reduction of suitable duck habitat would occur. The effort of the State, through the purchase of lands for duck refuges, to increase available habitat, while of relatively recent development, is of major importance in affording undisturbed resting and forage areas for the birds. Restriction of oil pollution of ocean, bay and stream waters, provision of fish ladders over irrigation and power dams and of fish screens at entrances to irrigation canals have been subjects of importance in fish conservation.

Much of ecologic importance is involved under heading "B" in the direct efforts to control and manage wild life. Research leading to a full understanding of the life history and ecologic requirements of each species and the gathering of data to indicate whether or not the annual levy upon wild species is leading to depletion of breeding stocks are obviously the foundation stones upon which any program of game administration must rest.

These foundations have often been unappreciated or discounted by wild life administrators through ignorance, selfishness or an egotistical belief in

their own omniscience, but there are some conspicuous instances where a sound basis for administration has been established. And, with rapid depletion of game supplies in many parts of the United States, attention is of necessity being forced more and more to the fundamental aspects of the subject. Exact biological knowledge of the ecologic and economic relations of any presumed "pest" should precede the outline of any control measures. Such knowledge has not always been at hand in past programs but its importance is being recognized increasingly. Planting of food crops for the especial benefit of wild species, efforts to propagate and distribute native or alien species, and the selection of wild life refuges all require a large amount of basic ecologic data, of which there is yet a scarcity.

Investigation and the accumulation of data on the annual levy exacted of wild species has been carried on in California most actively by the Bureau of Commercial Fishes of the California Division of Fish and Game. In 1919, by legislative enactment, a system of triplicate receipts between fishermen, wholesalers and the State was inaugurated which gives a detailed record of the kind, amount and price of fish taken for commercial purposes. Commercial fishing licenses and a tonnage tax on canneries have provided funds for prosecution of basic research on food fishes, and a large body of knowledge has been provided on the life history and ecologic requirements of fishes and molluscs. The annual take of deer was estimated by various agencies for many years, but in 1927 a system of deer-tags was established which provides a much more nearly exact record. A crude approximation of the take of fur-bearers is gathered in reports of licensed trappers, but is manifestly far from complete. The numbers of coyotes and wild-cats killed each year by state and federal agencies are recorded and data on mountain lions are available. The last, by reason of bounties offered by the State, is perhaps more nearly an exact record than any other body of statistical data relating to the kill of a wild species. No accurate appraisal of the annual crop of sport fish, water fowl or upland small game is possible.

The killing of predatory mammals and birds, in efforts to protect domestic livestock, is believed to have played a part in the unbalancing of conditions with respect to rodents and deer. The control of rodents by distribution of poisoned cereals is known to have killed some birds although details are scarce and much controverted as to numbers killed and as to the ultimate effect on local bird populations. Gassing of rodents in burrows leads in some cases to destruction of other species inhabiting these burrows for shelter. Planting of agricultural crops has augmented the potential food supply of certain wild birds and mammals, both game and non-game species, which have resorted to these supplies and species have bred up to greatly increased numbers with the result that damage and losses have been experienced locally by certain growers of these crops. Planting of food supplies intended directly to benefit wild species, especially game birds, is, as yet, of negligible importance in California. Extensive efforts to augment the game supply by

acclimatizing the ring-necked pheasant and a few other species of game birds have been made, with a total recorded expenditure of over \$200,000 to date, without significant results, for sportsmen. [Data from California Division of Fish and Game, 1891-1931.] Several freshwater fishes from eastern North America have, on the other hand, been successfully acclimatized so as to provide much sport and commercial fishing of satisfactory character without supplanting desirable native species to any appreciable extent, so far as known. Establishment of wild life (especially game) sanctuaries is still in the experimental stage; problems of location and character and degree of "management" are numerous and diverse in this field.

THE DEER PROBLEM

Space will not here permit detailed analysis of ecologic factors for many species, so attention will be concentrated on ecologic problems involving the native mule and black-tailed deer.

The native deer constitute an important element, esthetically and economically, in the wild life of California. The presence of deer adds attractiveness to the out-of-doors, a factor of importance with increased travel in recreational areas. The economic importance of deer in California has always loomed large. From the time of the first white travellers and settlers, deer have been levied upon for food and for sport. At one time (about 1880) there was an enormous traffic in deer skins which greatly reduced the wild stock at least locally. Protective legislation, with bettered enforcement, now controls the kill for sporting purposes until it is believed that the annual levy from this source is not reducing the wild stock. Between 1911 and 1916 the reported kill was from 6500 to 8700, with an estimated total of 12,000, annually (Hall, '27, p. 246). Since 1927 when the deer-tag license law became effective, the sale of tags has exceeded 100,000 yearly, and a kill of around 20,000 annually has been reported, reaching 25,805 in 1931. To this must be added the legal killings not reported and the illegal killings which go on throughout the year in the sparsely settled mountainous portions of the state, so that the total annual kill of deer in California is certainly not less than 30,000. Despite this large annual toll the deer population is not declining in numbers although changes may be occurring in the sex ratio and in the average size of adults. In fact, some persons believe the total deer population is actually increasing.

So long as deer restrict their foraging to native vegetation on uncultivated public or private lands, their presence may be considered largely, if not wholly, beneficial. A few live-stock owners complain of the wild forage taken by deer which might otherwise be harvested by domestic animals, but this item is a local and minor one. However, when deer begin to forage on trees, vines, truck and field crops planted and cultivated by man, their presence becomes a matter of economic concern. A survey of deer damage

throughout California in 1930, conducted by the author and Mr. G. H. True, Jr., of the California Division of Fish and Game, brought 297 reports from 53 counties of which 246 from 45 counties described damage in various amounts (Storer and True MS, '30; True, '32). These reports, gathered from agricultural commissioners, forest officers, and game wardens, reveal difficulties with deer wherever agriculture borders or has invaded deer range. Forty-six specific crops were mentioned, damage to truck gardens, vineyards, and young orchard trees being mentioned most often. In Eldorado County, a careful study of damage by deer to orchards was made by the farm advisor. Of 300 questionnaires issued, 98 were returned, and 89 farmers reported damage. Costs of tree replacements or retardation were evaluated with data provided by the University of California. The gross damage aggregated over \$19,000 for trees killed and over \$27,000 for trees retarded in growth. Eighty per cent of the damage in this county has occurred within the past five years. Accounts from other portions of the State indicate increased damage in recent years. Although numerous specific records and conservative estimates have been furnished, no satisfactory financial appraisal of the damage over the entire state can be made. It certainly amounts to many thousands of dollars annually.

Only a part of this damage occurs on so-called marginal farms of dubious economic status. Abandonment of such farms will not mitigate the trouble by any means. Much excellent agricultural land in California is in hill country on cleared or cut over land or in valley bottoms adjacent to normal deer range. In Santa Cruz County alone there are 2,200 farms, of which 70 per cent are on cleared or cut-over lands, mostly in hill country. Damage occurs on bona-fide farms, and is likely to continue unless satisfactory adjustments in administrative practice are forthcoming. Permissive killing of deer causing damage and deer-proof fencing (Storer and True, '31) financed co-operatively by state and land owner, are experiments legalized by the 1931 Legislature and now under trial.

It seems appropriate, therefore, to enquire into the causes which have been operative to bring increasing damage in the face of a reported doubling or trebling of the annual kill of deer by hunters in the past fifteen years. Several factors of ecologic importance are present.

Systematic killing of mountain lions has been practiced in California for many years. Data for early years are lacking, but since 1907 a system of state bounties has been in operation and from 1918 on the Fish and Game Division has employed one or more official lion hunters. A total of 5811 lions was submitted for bounties from 1907 to 1929 inclusive; the annual toll is now over 300 (*California Division of Fish and Game, Bienn. Rept.*, 31, 1931, p. 173). Beginning in 1916, systematic effort under joint state and federal auspices has been directed against coyotes and wild-cats in California, first to reduce rabies infection in the northeastern plateau counties, and latterly at the behest of live-stock owners, particularly sheep men. In a ten

year period ending in mid-1931, a grand total of 39,835 predatory animals had been "officially accounted for" as killed by control operators of the California State Department of Agriculture and the U. S. Bureau of Biological Survey (Poole, '31, p. 469). To these must be added an unknown number taken by private agencies for fur or otherwise. Coyotes are now so greatly reduced that a recent official estimate places the losses among sheep at not over one per cent (Poole, '31, p. 468). Coyotes are now actually scarce in many places where a decade or two ago they were common. These three carnivores are known to levy upon deer. A classical estimated minimum of one deer per week has been stated for the mountain lion; the numbers killed by the other two are unknown. It should be emphasized that coincidently with the decrease in these carnivores, damage to crops by deer has been increasing. However, this reduction in predators is not believed to be the only factor in the increase of damage by deer.

A second item requiring attention in the deer problem is the policy of forestry officials in restricting burning on forest and chaparral areas. According to old-time residents, in foothill areas especially, fire was of common and repeated occurrence in earlier years. There were numerous small fires which ran only short distances and then died out, there being less accumulation of inflammable material then than now. It is reported that old-time hunters used to set fires on purpose. These older residents report that under the burning practice then in vogue the "brush" (chaparral) was of more open stand and of lower stature making it possible for a person or large animal to go anywhere on hillsides which now, since burning is restricted, are covered with impenetrable growths of dense, tall chaparral. With the earlier restriction of chaparral herbaceous vegetation was more plentiful, but since burning has been prohibited herbaceous vegetation and grasses are screened out by the growth of the chaparral. Earlier, deer are reported to have stayed on the chaparral slopes and not to have invaded cultivated lands, even when the latter were unfenced.

There is incontrovertible evidence of the frequent occurrence of fire in the vegetation of many parts of California during the pre-historic period. Many species of forest trees have fire-resistant bark, certain pines release their seeds only in the presence of fire, the seeds of some chaparral plants are stimulated to germination by the heat of fire, and certain chaparral species regularly send up stump sprouts following fire.

Closely related to the factor of fire is that of mineral balance in wild forage crops on range lands, an important problem now engaging much attention by students of animal nutrition. During the past two or three decades the importance of small but definite amounts of certain mineral constituents in the diet of animals, especially of ruminants, has been more fully recognized. These minerals, besides providing for skeletal structure, influence general growth and reproduction, and are believed to play a part in the resistance of animals to parasitic and infectious diseases. All details of the

minera. balance are not yet fully understood, but enough has been learned to show the very necessary place of these elements in the food.

Deficiencies in certain essential minerals have been found in many places over the earth, particularly in arid regions; conditions obtaining in parts of California are duplicated in India, Australia, and South Africa (Orr, '29). That mineral balance is as important for deer as for domestic ungulates can scarcely be doubted; in fact, shreds of evidence are already accumulating which point definitely in this direction.

When fire sweeps an area covered with vegetation the latter is reduced largely or completely to mineral ash. The ash is shortly dissolved and carried into the soil where it becomes available for plants, especially those with superficial root systems. Where plants grow for a period of years without being burned, only a limited amount of the mineral substance is returned annually in the leaf drop. When burning occurs the mineral in the surface débris as well as in the woody portions of plants is returned and made available for new growth.

For many years cattlemen have observed that their stock exhibited a particular preference for foraging on areas recently burned over. Similar observations have been reported for deer. In Lake County deer foraged for several years in certain cultivated alfalfa fields. Then fire swept an adjacent chaparral slope and the following year the deer remained to forage on the hillsides and did not bother the alfalfa. Research by the staff of the Division of Animal Husbandry of the University of California has shown that in the Sierra Nevada, *Ceanothus integerrimus*, which is a browse plant sought by both deer and cattle, undergoes a seasonal change in the calcium-phosphorus ratio with seed maturity (this change occurs in other plants as well); the shrubbery then is less sought after by cattle. But on an area which has been burned over the animals apparently seek this forage through a longer period and show a strong preference for it. The same is true of herbaceous cover such as filaree, which often springs up in dense tall growth following fire.

These observations are not to be taken as a whole-hearted argument for burning by individual property owners or for wholesale burning under governmental supervision, but are presented to suggest the nature of some of the ecologic factors involved in the food habits of a wild species under man-made alteration of the environment.

Attention thus far has been directed to the withholding of mineral from the soil and from the animals by plants. But certain of our game and agricultural practices, more particularly the latter, are tending actually to deplete the supplies of available mineral in our grazing and browsing lands. Under original conditions a more or less closed food chain existed of *minerals-herbaceous and shrubby plants-grazing and browsing mammals-carnivores-minerals*, etc. Mineral substances were passed from soil to plants, through one or more animal species and then returned to the soil through death and

decay of animals at the end of the food chain. Such toll as the Indian population levied was local and game taken for food was consumed close by. With the advent of Caucasian settlement an export of animals, and, incidentally, of mineral substance, particularly from hill and mountain regions, was initiated and this has now gone on for upwards of 60 years in California. The aggregate drain by removal of game animals (chiefly deer) is not serious and alone would probably constitute no cause for concern. But from early days a migrant pasturing scheme with sheep and cattle has been practiced in California and likewise in other mountainous regions of the arid American west. Herds of domestic livestock are wintered on lowland pastures, driven to the mountains for subsistence and growth during the summer season and again returned to the lowlands. The seasonal increment in mineral substance in bones and soft parts is thus permanently removed from upland and montane forage areas and never returned.

The only means for mineral replacement in upland areas are the slow processes of rock weathering and soil formation, in the latter of which burrowing rodents play a considerable part in arid regions. In this connection current efforts at rodent control on montane pastures which effect a temporary increase in the crop of herbs and grasses that may be harvested at once by domestic stock, need to be scrutinized closely to determine whether greater permanent benefit accrues through the temporary enhancement of the plant cover or through the original ecologic relations where rodents aid in formation, cultivation and aeration of the soil.

Demineralization of upland areas also results from the washing down of dissolved materials in streams; the relative importance of leaching by rain and snow waters and of the removal by migrant livestock cannot be evaluated at the present time. In other portions of the world, the depletion of minerals in pastures has proceeded to such an extent as to engage serious attention by students of the soil and of animal nutrition, and we are already being forced to a consideration of the problem in California. The relation of mineral deficiency on wild lands to the attacks of deer on cultivated crops while yet to be demonstrated by adequate scientific experiment, is suggested by some observations already accumulated. If this does prove to be one of the important factors, then some radical treatment of the mineral balance problem will be required. A further topic for study is that of the relation of mineral supply to reproduction in deer. Certain persons claim that a percentage of the does in parts of California are "barren" and that such does do not contribute to the fawn crop upon which the supply of bucks for legal hunting is dependent. The authenticity of this claim has been questioned by other persons. The subject needs study in the light of work done on domestic livestock on the range by Hart and Guilbert ('28).

It would seem, therefore, that "solution" of the deer damage problem cannot be had either by permissive killing or by fencing, but is intimately related to human activities in the fields of animal husbandry and forestry.

Finally, there have been several instances of epidemic disease among deer in California. Scarcely any of these epidemics have been studied adequately. In 1924 foot-and-mouth disease was transferred from migrant cattle to mule deer on the west flank of the Sierra Nevada at the north of Yosemite National Park. Radical operations to eliminate the disease involved the killing of 22,214 deer, of which 2279 showed evidence of infection (Keane, '27, p. 225), before the area was safe for healthy animals once more. Deer may possibly exchange parasites with domestic ungulates, besides which are the diseases peculiar to deer of which little is known as yet.

Thus the "deer problem" in California involves a conflict of interests. Aid to livestock owners through predatory animal control is prejudicial in a degree to producers of orchard, vine, field, and truck crops, through release of pressure by carnivores on the deer population. Use of forest lands to produce timber, livestock forage, game forage and cover and to husband water again results in an interaction of diverse human groups. There is definite need, therefore, to link all groups concerned in the management of uncultivated lands, of plant cover, of domestic animals, and of wild animal life.

CONCLUSIONS

In concluding this brief catalogue of factors influencing wild life in California and the presentation of an example of the complex ecologic problems involved in the management of a single wild species, I should like to stress the four items essential to adequate supervision of wild life in any region.

1. Integration of the several interested human groups (agriculturists [both livestock and crop production groups], foresters, irrigationists, naturalists, public health agencies, sportsmen, conservation agencies, etc.) into a common forum for well-rounded consideration and analysis of the problems.
2. Insistence that the proper "solution" requires adequate study from the ecologic standpoint, to determine the factors involved and their relative importance, and that only properly trained biologists can carry such studies to satisfactory completion.
3. Necessity for developing adequate research facilities by agencies charged with wild life administration and that these facilities should be free of political influence and sufficiently stable to attract competent personnel: financing of research programs in universities with funds from wild life conservation agencies provides an appropriate basis for sound and stable research programs.
4. Final adjustment of practice to the most equitable balance between conflicting human interests, after adequate study of each problem.

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IS THE LONGLEAF TYPE A CLIMAX?

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What is a climax? The commonly accepted definition is, a type of vegetation which has adapted itself over a long period to a set of environmental conditions, so completely that it is stabilized as long as those conditions remain unchanged.

In a narrower sense, a climax type assumes adaptation to a *given set* of conditions excluding other conditions. The conditions excluded are those which would usually result in disturbance of this stability or equilibrium. These are; fire, under the conception that fire acts to destroy the stand; insects, when epidemic; destructive winds. The effect of *imported* diseases and insects, or of man's interference in lumbering, destroys the balance and the type may completely change. Climax types may therefore yield at any time to new conditions to which they are not adapted. Excluding the above factors, there would remain only the climatic and soil factors of site. These factors, isolated from the effects of the so-called destructive group, would finally establish a forest type in which the only surviving species would be those capable of enduring the shade of a forest cover during their establishment. This condition necessitates the elimination of fire, wind, insect epidemics and disease for periods longer than the life span of species which cannot endure shade. When, as with Douglas fir, this span is from 300 to 500 years, and the environmental conditions are such as to create extreme conflagration hazard at intervals of from 3 to 10 years, the establishment of climax types of more shade-enduring species, which are usually inferior in utility, is a pure accident. In the life span of the species, any factor, such as fire, which can be depended on to occur even once within that period, and create conditions favorable to its reproduction, may become the determining factor in its perpetuation as *against* shade-enduring or so-called climax types. The characteristics of such a relationship are that while fire is required (or its man-made substitute, lumbering) for the removal of the overwood shade and establishment of reproduction, the total exclusion of subsequent fires is equally necessary for survival of this reproduction. The distribution and composition of the forest types in such a region is, therefore, very irregular, much young growth is destroyed prematurely, and here and there a patch may finally attain the climax or shade-enduring type.

If for any reason the normal or natural frequency of fire is increased so that its chance of occurrence on any given area becomes once in 10 to 15 years, the only hope for survival of the tree species is ability to develop a fire resistant bark within such a period and the fact that the fires when they do occur will

burn at such times as not to create excessive heat, nor find sufficient fuel to make a blaze destructive to this bark and cambium, and finally, that the crowns of the trees escape fire. These conditions are found, very imperfectly developed, in hardwood species, but most of the southern pines seem well adapted to a fire frequency of this sort. Loblolly, slash, and shortleaf pines, three of the four commercial southern species, rapidly attain a diameter and bark thickness which at 10 years of age enables them to survive the average fire, if it occurs during the winter or early spring and the trees are growing on their normal sites which produce considerable hardwood brush or shade and not much coarse sedge grass. But if fires burn at abnormally frequent intervals on such types, as occurs usually after logging, the young reproduction from 10 years and under is apt to be exterminated and the pine replaced by persistently sprouting and more fire resistant oaks.

On such types, it is probable that fire might with advantage be permanently excluded, though there is evidence which indicates that removal of logging slash by fire, in addition to removing this terrific initial hazard, reduces the competition of hardwood brush with pine seedlings not yet started, and thus increases the percentage of pine in the next crop. It must be emphasized, therefore, that a forest type is the form of vegetation which is best adapted to survive not merely a few selected conditions like soil and climate, but *all* the conditions which will arise over the entire period or span of life of the individual trees of which it is composed.

We must now consider the longleaf pine, *Pinus palustris*, type of the southern coastal plain. This type constitutes a practically 100 per cent pure stand of a single species. It occupies soils of several types, varying from deep sands to fine silt underlaid by clay or hard pan. These longleaf pine sites do not support a natural growth of the better hardwood species. On the richer grades of soil, rather generally throughout the range of the species, southern red oak, *Quercus rubra*, is found mixed with the pine and occupying the cut-over land. Another common associate is the black jack oak, *Q. marylandica*, which is confined to dry sites and is often completely absent from large areas in the more southern portion of the range. On the poorer sites, *Q. catesbeai*, *Q. cinerea*, and *Q. geminata* are found. These scrub oaks are partial to deep sand and are frequent in Florida. On such sites grass vegetation is sparse.

Throughout most of the northern and western portions of the range of the longleaf pine the natural ground cover is predominantly species of *Andropogon* or *Carex*. The presence of legumes is apparently encouraged by occasional burning. Wire grass, *Aristida stricta* and *Muhlenbergia* sp., largely takes the place of *Andropogon* in the more southerly and especially in the eastern portion of the range, in southern Georgia and Florida. In the absence of fire the dead sedge grass or wire grass accumulates into a mat or mulch of dry material which does not decay readily and may be at least six inches thick. Fires run readily in the dead grass on any dry day in winter or spring, summer or

fall, even with a single year's accumulation. The fire hazard steadily increases, probably up to the 10th year, and does not diminish thereafter for an unknown period. With the possibility of fire every year, it is extremely probable that even without the aid of man, fires set by lightning might occur in this type as frequently as 3 to 4 years apart and burn over large areas, and, as the type occupies the better drained lands and ridges and is not found in stream bottoms, few continuous natural barriers would intervene.

None of the other southern pines which might grow upon such sites can endure fires of this frequency in their seedling stage, and this reason alone would account for their entire exclusion from the longleaf pine type.

By contrast, the longleaf pine is completely adapted to this frequent fire interval, and has for this reason taken exclusive possession of an area of approximately one-half of the entire coastal plain from Virginia to Texas. As long as the prevailing conditions which created this pure type continue, the longleaf pine type is as truly a climax as the beech-birch-maple type in the northern hardwoods. This conclusion is based on four presumptions of great importance in handling this vast area for forest production; first, that frequent fires at intervals of considerably less than ten years are a natural condition which must be met by any species in order to survive on these sites; second, and perhaps more important, that germination and establishment of the seedlings of this fire resistant species is dependent almost absolutely on the occurrence of fire previous to the fall of the seed; third, that fires occurring during the juvenile period previous to the initiation of height growth are necessary for survival in the presence of competing species of pines and hardwoods; and fourth, that fires during the same period may have an important influence in reducing damage from the brown spot disease.

The fire resistance of the longleaf pine has long been evident even to the layman. It is due, first to its habit of concentrating all its growth for an initial period averaging five years in the root and during this time making no height growth; second, to its ability, through food stored in this root, to put out new needles in the spring after the existing foliage has been entirely killed by fire; third, to the protection of its bud or growing point from killing heat, afforded by the dense circular tuft of green needles surrounding this bud; fourth, to its abnormally thick and fire resistant bark as soon as height growth commences; and fifth, to the sparseness of its branching as a young sapling, which discourages crown fires. Remarkable recovery and persistence of growth are shown even in the presence of annual spring fires. An annual fire frequency, however, does not appear to be natural or beneficial. Growth may be stunted and the seedling finally killed. The seedlings germinate and are established in the fall and are destroyed by a fire during that winter or spring unless they happen to grow where the grass cover is thin, when the flames may pass them by, owing to the complete absence of stem and the resultant effectiveness of the protection given to the bud, which is close to the ground and surrounded by a rosette of needles. Up to about 1915 prac-

tically no areas of longleaf pine had been purposely protected from fire, and where the species had failed to reproduce itself, the causes were, destruction by hogs, removal of all seed trees, and annual fires, all unnatural and destructive of the normal balance.

It was not until fire protection had been attempted in certain regions that the statistical, scientific evidence became available which has since demonstrated the remaining factors, indicating the dependence of the species on frequent fires for its survival. The conclusion that the species owed its existence and survival to fires and would disappear were it not for the continuance of fire was definitely stated by Mrs. Ellen Call Long in 1888 and by Dr. Roland M. Harper in 1911-13, and this possibility was at least strongly suspected by Sir Charles Lyell in 1849, who stated in his "Second Visit to the United States," (p. 69), in speaking of the vicinity of Tuscaloosa, Alabama, "These hills were covered with longleaved pines, and the large proportion they bear to hardwoods is said to have been increased by the Indian practice of burning the grass; the bark of the oaks and other kinds of hardwoods being more combustible, and more easily injured by fire, than that of the fir tribe. Everywhere the seedlings of the longleaved pine were coming up in such numbers that one might have supposed the ground to have been sown with them; and I was reminded how rarely we see similar self sown firs in English plantations."

At Urania, La., on the lands cut over for longleaf pine and protected since 1915, the Yale Forest School established over 100 plots in 1917 and following years, on which a detailed record of seedlings, their establishment, survival and growth has been kept. The following relationships were determined in the order mentioned:

1. On land burned annually for many years previous to the fall of seed, abundant seedlings were established, and even under subsequent complete fire protection these seedlings began height growth in the fifth year and developed normally, provided they were free from competition of loblolly pine or vigorous oak brush.

2. Wherever other pines or oak germinated or sprouted in the same year, i.e. after the last fire, these competing species, in the absence of further fire, in every case suppressed the longleaf pine and prevented its height growth, ultimately causing its death after about 15 years.

4. On land protected from fire since 1915, new seedlings germinated from seed crops of 1917, 1920 and 1921, 1926 and 1929, but in *steadily decreasing numbers*. Such seedlings as came up were always found on bare spots or where the radicle could reach mineral soil, and practically never in the unburned dense litter of dead bunch grass or wire grass.

4. The seedlings of the 1917 crop, 2 years after fire protection, came through in many instances and developed normally.

5. The seedlings of the 1921-22 seed crops, 6 to 7 years after fire protection was established, at ten years of age, have failed for the most part to

begin their height growth, even when free from all tree and brush competition. They remain stunted and are slowly losing vigor. About the 15th year they will probably die out, though here and there one struggles through.

6. The seedlings of the years 1926 and 1929, 11 to 14 years after fire protection was started, seldom survived the first season and failed to establish themselves.

It thus appears that 5 to 6 years of fire protection will so alter the ecological conditions that seedlings if established cannot compete with the sedge and grass vegetation. Continuation of fire protection for 10 years or more prevents, for the most part, the germination and establishment, and cuts short the survival to a period of a year or two, all this in the complete absence of competing brush or tree species.

The dependence of the species on fire for its establishment was shown in still another way. On areas protected from fire and containing numerous seedlings both in the grass and in the initial stages of height growth it was noticed in 1922 that a virulent needle blight now designated as the brown spot, *Septoria acicola* (Thüm) Saccardo, Syl. Fung., 3: 507, 1884, attacked and defoliated the pines which had not yet reached a height of over 3 to 4 feet. The foliage beyond this height was not affected, hence the damage was confined largely within the zone that would normally be reached by grass fires. A delicate balance of atmospheric moisture and sunlight appeared to control the infection. The freer movement of air at the greater heights above the ground, and the greater dampness or higher relative humidity near the grass zone and soil surface, thus shaded, appeared to be the favorable factors. The disease did not defoliate or seriously infect young pines when growing under considerable shade. Their later death was from suppression, instead. The infection was worse, apparently, in rainy than in dry seasons. Pines which had started their height growth were killed in three years, but a large percentage of these vigorous saplings escaped. The seedlings in the grass stage were partially defoliated annually where infection was severe, but persisted, in a more and more enfeebled condition, for ten years. There is but little hope of their ultimate survival or recovery but if fires can be kept out long enough, the fate of the seedlings will finally be demonstrated.

The significant fact, however, is that fires have occurred here and there during this period, and in every observed instance, the foliage put forth following the fire was healthy and vigorous and free from the disease during the first season. This release from defoliation by the brown spot enables the seedling to carry this foliage over into the second year. Whenever this happens, a great accretion of vigor is noticed. This is true whether the retention of the foliage be due to absence of fire during the intervening winter or to the disinfection of the area caused by the initial fire.

During the second growing season following a fire, the disease begins to reappear but is not serious. In the third year, it may be very bad again, depending probably on several factors, one of which is the presence of unburned

infected areas nearby. So prevalent were fires before the advent of efforts at fire prevention in the South that the existence of this disease was not generally known to land owners until within the last decade, though it was first described in 1884, and was observed by foresters in 1916-18. As it is, the relation of control of the brown spot to the occurrence of fire at intervals of 1 to 3 years is one more evidence of the adaptation of this species to average prevalence of fire at frequent intervals, as an important ecological factor affecting the survival of this forest type.

Efforts to attain absolute fire protection in the longleaf pine and bunch grass type, besides defeating the basic purpose of silviculture, which is the perpetuation of the type, through securing natural reproduction, creates a fire hazard of an alarming character. Fires, if set in this accumulated "rough" during the summer or fall when the ground is dry often kill mature pine and are usually fatal to saplings under 12 inches, which are normally fire resistant. One bad fire, which might be set on any of a hundred days in any year might destroy the forest, while by conforming with natural ecological conditions and burning under control during damp weather, or at night, in the late winter, scarcely a needle would be scorched and the forest would be made safe for the next one or two years.

In the light of these facts the writer suggested ('26) that in order to favor the survival of longleaf pine seedlings the ground should be burned in the spring of the fourth year after germination, and again three years after if necessary. (This latter burning was advised as a measure of fire protection for the young saplings, then probably about 5 to 6 feet high.) In the longleaf pine type of the south (and nowhere else in North America to the writer's knowledge) fire at frequent but not necessarily annual intervals is as dependable a factor of site as is climate or soil. The conception of a climax type as one which has reached a stage of permanent equilibrium or perfect adaptation to these constant factors of site should include the longleaf pine type of the south, which presents by far the greatest area and most permanent characteristics of any climax to be found in the United States.

In conclusion, the statements made in this article while based upon continuous and extensive plot records must not be accepted in full as thoroughly established or applying without modification to the entire range of sites and conditions over which the longleaf pine is found. Studies by Paul V. Siggers of the Southern Forest Experiment Station showed that a single fire reduced the brown spot needle disease for the season following the fire, in three cases, respectively, from 61.5 to 21.1 per cent; from 17.8 to 0.2 per cent, and from 16.6 to 1.3 per cent. In two of these cases, the infection at the end of the second season was as heavy on the burned as on the unburned area, while in the third case it was but one half that on the unburned tract. On the two Roberts plots at Urania, La., annual controlled spring fires, first set in the second spring after the germination of the fall seedlings when the seedlings were 14 months old, did not kill a single seedling during five successive

fires, and the loss in a second series of five fires was no greater than that from natural causes, including brown spot disease in the adjoining unburned control plot. Each plot was one-fourth acre in size. Effectiveness of the use of fire as a disinfectant for this disease must be at least in part influenced by the thoroughness of the disinfection and the proper procedure indicated would be to burn all longleaf pine areas in the vicinity at the same time. Carefully planned experiments have now been initiated by the U. S. Forest Service and by the writer to test the effects of controlled fires, at intervals of 2 to 3 years, on the survival and development of seedling reproduction of this species. Through these experiments it is hoped that a silvicultural practice may be developed which will duplicate the natural conditions under which the longleaf pine has maintained itself for untold ages over the largest area in America occupied by a pure stand of a single species.

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STUDIES IN NOCTURNAL ECOLOGY, II. PRELIMINARY ANALYSIS OF ACTIVITY RHYTHM IN NOCTURNAL FOREST INSECTS¹

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It has been shown elsewhere that climax forest has a definite nocturnal fauna, the activity of which is in apparent correlation with the rhythmic expression of such factors as light intensity, temperature, relative humidity and rate of evaporation within the association (Park, Lockett and Myers, '31).

The present report is an attempt to study characteristic nocturnal animals, having their habitat niches on or near the floor, under experimental conditions, to further develop certain aspects of the more general problem of the forest at night.

THE NOCTURNAL ACTIVITY OF THE FOREST COCKROACH, *Parcoblatta pennsylvanica* (DEGEER)²

It is well known that roaches are usually nocturnal, hiding by day and feeding, mating and ovipositing by night (Haber, '20). Their abundance and wide distribution make them suitable as research material.

In the first series of experiments, the activity of *P. pennsylvanica* was studied under relatively normal environmental conditions. Two groups of roaches were placed in glass culture dishes having an inside diameter of eighteen centimeters and a depth of seven centimeters. The bottom of each dish was covered with moist soil and shelter was provided by bits of bark, wood and leaves. The dishes were placed on the wide window ledge outside of the laboratory. After an adjustment period of from one and a half to two hours, the number of roaches active in each dish, and not under shelter, was recorded every hour for from twenty-one to thirty-one hours. These data gave the percentage of individuals active at each hourly reading during the experiment. At night readings were made by flashlight, the bulb of which was coated with red ink. It may be said that under these conditions readings were made satisfactorily, with little visible disturbance of the animals. Each reading lasted about fifteen seconds.

Frequent repetition of this simple experiment clearly confirmed for this species the long established view that cockroaches as a group are nocturnal, *viz.* are active when the environmental factors are in the nocturnal phase of

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² We are indebted to Mr. Herbert H. Ross of the Illinois State Natural History Survey for determination of the cockroaches.

their cycle. A typical experiment of this type is graphed in the following figure (fig. 1).

In the second place, the influence of a constant environment upon the activity of *P. pennsylvanica* was studied. Twelve individuals were placed in culture dishes as noted previously, and these were set in a constant temperature cabinet. The latter was maintained at an air temperature of from 23.6 to 25.4° C., the range given being the extreme variation over a typical twenty-four hours. The air in the cabinet was held near saturation by several large, wet sponges drawing from a pan in the bottom of the chamber. Under these conditions the relative humidity was so high that the interior

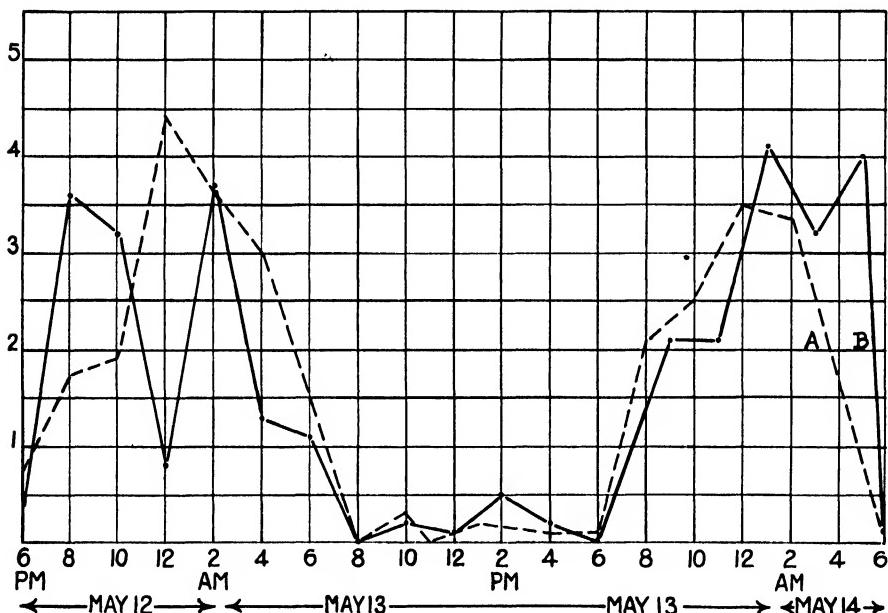


FIG. 1. Nocturnal activity of *Parcoblatta pennsylvanica* under relatively normal conditions. A = Percentage of cockroaches active; B = Air temperature.

of the cabinet was covered with a film of moisture and the glass observation port had to be coated with albumin to make readings possible. Standardized Livingston atmometers were connected by tubing to burettes outside of the chamber and gave an indication of this saturation. The average rate of evaporation was .1 c.c. per hour, and the average amount of total evaporation for twenty-four hours was 2.37 c.c. The cockroaches were in total darkness throughout this time, save for a fifteen to thirty second reading each hour when the observation port was uncovered and data taken by red light. Hourly readings, then, were taken of cabinet temperature, evaporation, and number of animals active. A control was run at the same time for the same number of individuals under relatively normal conditions, as described above.

A series of experiments was run under these controlled conditions, and a characteristic experiment and its control are graphed in figs. 2 and 3 respectively.

Finally, under normal conditions of light, temperature and humidity, roaches were marked differentially with white laquer and acted, on the whole, as did an equal number of unmarked control individuals under normal conditions. As would be expected, the marked individuals exhibited individualities within the general species activity type. Some became active regularly before others; some were active at all observations; some markedly less active at night than others.

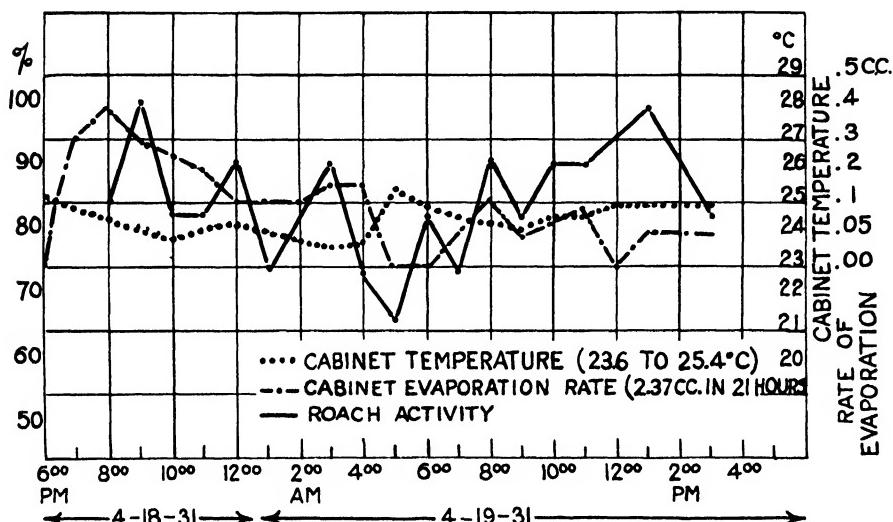


FIG. 2. Activity of *Parcoblatta pennsylvanica* in continual darkness, under constant temperature and rate of evaporation.

From these data we conclude that the forest cockroach, *Parcoblatta pennsylvanica*, appears to have its period of activity correlated with, and controlled by, the nocturnal expressions of the factors operating. Roaches are known to be normally photonegative, and it is probable that darkness is the most important single condition, and that in continuous darkness, their activity is maximal until fatigue sets in.

THE ACTIVITY OF NOCTURNAL FOREST COLEOPTERA

In addition to the forest cockroaches, the activity rhythm of a number of beetles was observed. The method of procedure was identical with that used in studying the roaches under normal fluctuations of daylight (*vide supra*). Two families of beetles were studied, Carabidae (*Amphasia interstitialis* (Say), *Chlaenius sericeus* Forst., *Clivinia impressifrons* Lec., *Patrobis longi-*

cornis (Say), *Platynus extensicollis viridis* (Lec.) and *Poecilus lucublandus* (Say), and Staphylinidae (*Staphylinus violaceus* Grav.).

All of these species were found to be normally nocturnal, spending the day beneath available shelter, and actively searching for food (e.g. earthworms and elaterid larvae) at intervals through the night. This is in general agree-

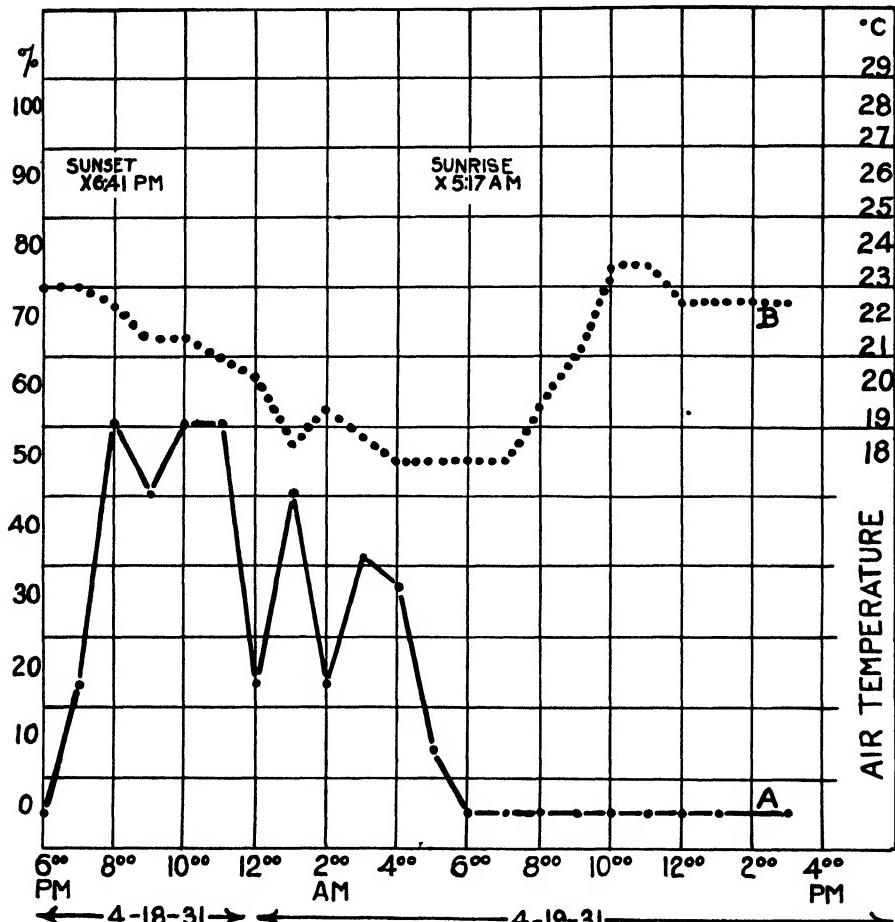


FIG. 3. Nocturnal activity of *Parcoblatta pennsylvanica* under relatively normal fluctuations of light, temperature and rate of evaporation. A = Percentage of cockroaches active; B = Air temperature.

ment with the findings of other workers. The Carabidae as a whole, with but relatively few exceptions, are a nocturnal aggregate (Blatchley, '10; Champlain and Kirk, '10; Garnett, '20; Oertel, '24; Chapman, *et al.*, '26; Kirchner, '27). As an example of the activity sequence of these forest floor inhabitants, four twenty-four hour experiments on the common carabid, *Patrobus longicornis*, are summarized in fig. 4. From the several graphs in this figure it

will be seen that the activity of the beetles began near dusk and continued intermittently until dawn. This confirms results obtained previously with other species under natural forest conditions (Park, *et al.*, '31). Wholly similar data were obtained for the other beetles listed above. In the case of *Clivinia impressifrons*, which is a geocole, commonly burrowing in wet floors near streams, activity was measured by their appearance at the mouths of their burrows, as well as walking over the wet surface of the soil.

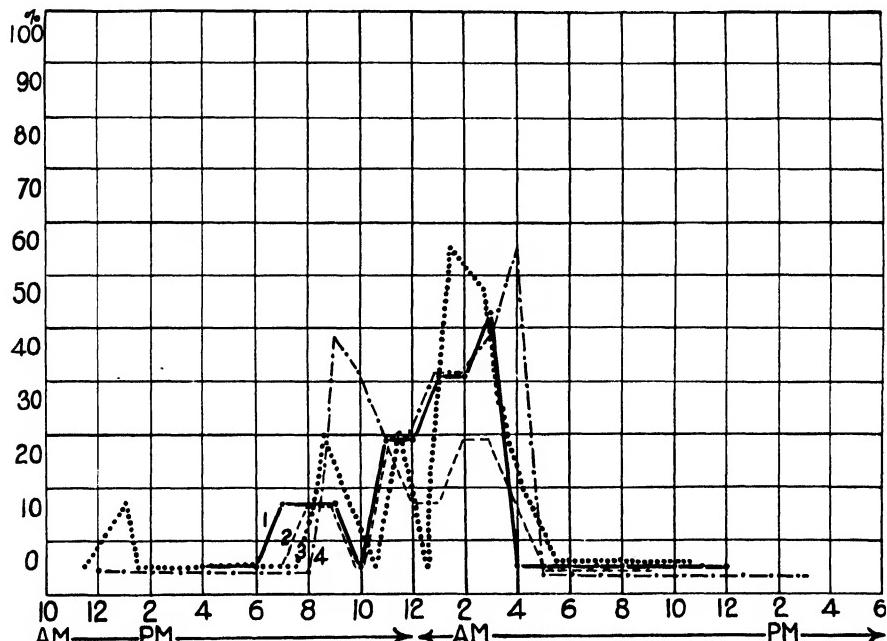


FIG. 4. Nocturnal activity of *Patrobus longicornis* under relatively normal fluctuations of light, temperature and rate of evaporation. Eight individuals were observed on four different nights: 1 (April 14-15); 2 (April 16-17); 3 (April 13-14) and 4 (April 18-19, 1931). The four records indicate the percentage of individuals active as a given time.

In fig. 4 it is seen that about half of the *Patrobus longicornis* were active each night. To determine how much of this activity was due to individual behavior, four of the eight beetles were marked differentially with white laquer. The remaining four were left unmarked to serve as a control for any possible deleterious effects of the paint. The controls gave the typical curve of activity for this species. The marked animals showed expected variability (fig. 5). Some were very active one night and tended to show little activity the following night (fig. 5, No. 2). None were active during the day, and in general each beetle left its niche at least once each night, presumably in search of food as they fed freely upon earthworms during this time.

THE NOCTURNAL ACTIVITY OF *Boletotherus cornutus* (PANZ.)

The cockroaches and beetles studied so far are essentially carnivorous. The present section deals with an herbivorous tenebrionid, *Boletotherus cornutus*. This abundant mycetocole is widely distributed over the area east of the Mississippi river. A characteristic inhabitant of forest, especially the climax, it may be had in numbers from its habitat niche, e.g. species of polyporoid fungi, especially *Polyporus* and *Fomes*, or beneath bark of logs and stumps near the latter (Weiss, '20a, b; Weiss and West, '20; Park, '31), where it is typically nocturnal, feeding and copulating at night (Park *et al.*, '31).

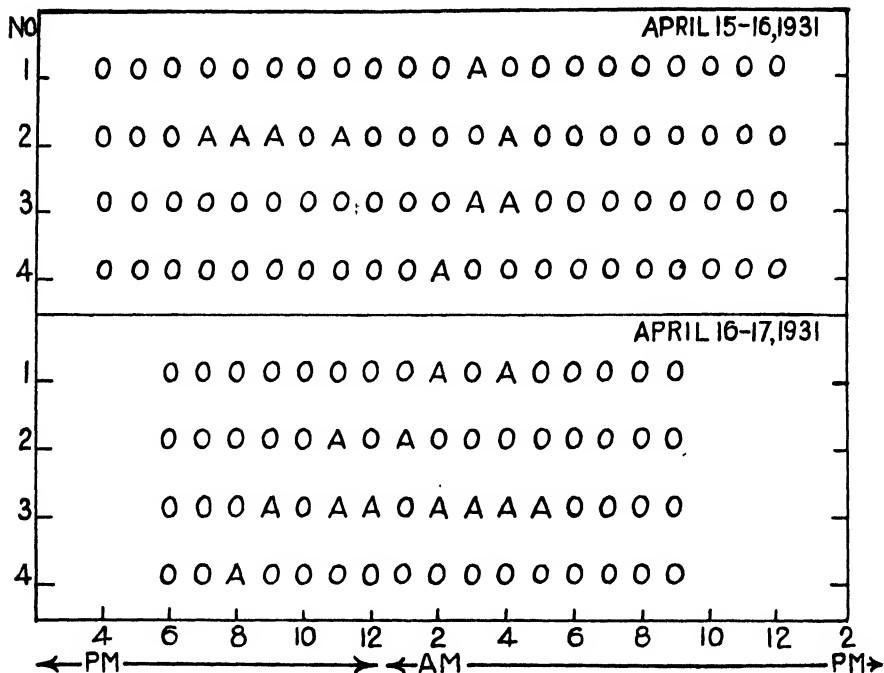


FIG. 5. Nocturnal activity of marked individuals of *Patrobus longicornis* on two successive nights under relatively normal conditions.

Two groups of *cornutus* were used. One was obtained from a climax maple forest near Joliet, Illinois. These were taken in the larval stage, on Feb. 22, by carrying the fungi (*Fomes applanatus*) back to the laboratory. Adults were reared from these larvae in complete darkness, *viz.* the larvae, pupae and imagines had never been exposed to daylight, and consequently to the illumination rhythm, acting on the forest community in nature. The second group of beetles was taken in the adult stage from the same species of fungus in the beech, maple, hemlock climax at Turkey Run State Park, Marshall, Indiana, on May 10.

Ten beetles of each group ($5\delta\delta$, $5\varphi\varphi$) were marked differentially with white paint, and each group was placed in a large evaporation dish as used previously, the bottom of which was covered with a circular piece of paper which had been ruled off into inch squares, each square numbered. The two dishes were placed in the constant temperature chamber, and hourly readings taken of temperature, evaporation and the distance each individual was found from its location of an hour before. The chamber was in total darkness save for the thirty seconds of each hour when readings were taken. From the data obtained, the distance moved per individual per hour could be calculated, assuming that an individual moved in a straight line from the center of one square to the center of another square upon which it was found. The distance traveled was the least the insect could have covered, obviously, so that the results may be taken as conservative, although the species is a slow, deliberate walker.

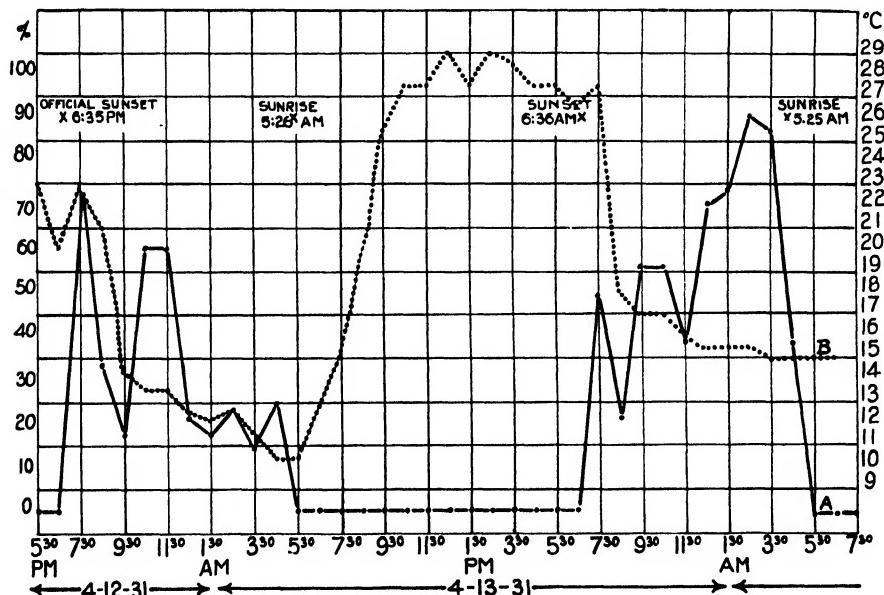


FIG. 6. Rhythmic activity of *Boletotherus cornutus* in total darkness, with temperature and rate of evaporation held constant. A = Beetles collected in forest were adults (imagines); B = Beetles collected by transporting fungi and rearing them in the laboratory in continual darkness. The periodicity indicated in the two curves was operating in total darkness, an air temperature of between a total range of 24.3 to 25.5° C., and a constant rate of evaporation of 0.1 c.c. per hour.

Figure 6 gives the record of a typical experiment, and four of the twenty-four hour experiments are summarized in fig. 7. From these two sets of graphs it will be noted that, notwithstanding the total darkness and constant temperature and evaporation of the environment, the mycetocoles were active

during the night and inactive during the day. This activity rhythm has been demonstrated for the same species under natural habitat conditions (Park, *et al.*, '31), and the results obtained are very interesting from at least two points of view. Firstly, because both sets of beetles gave the characteristic nocturnal response, although one group had never been exposed to alternating daylight and darkness. Secondly, the nocturnal-diurnal rhythm was not exhibited by forest cockroaches under the same experimental conditions.

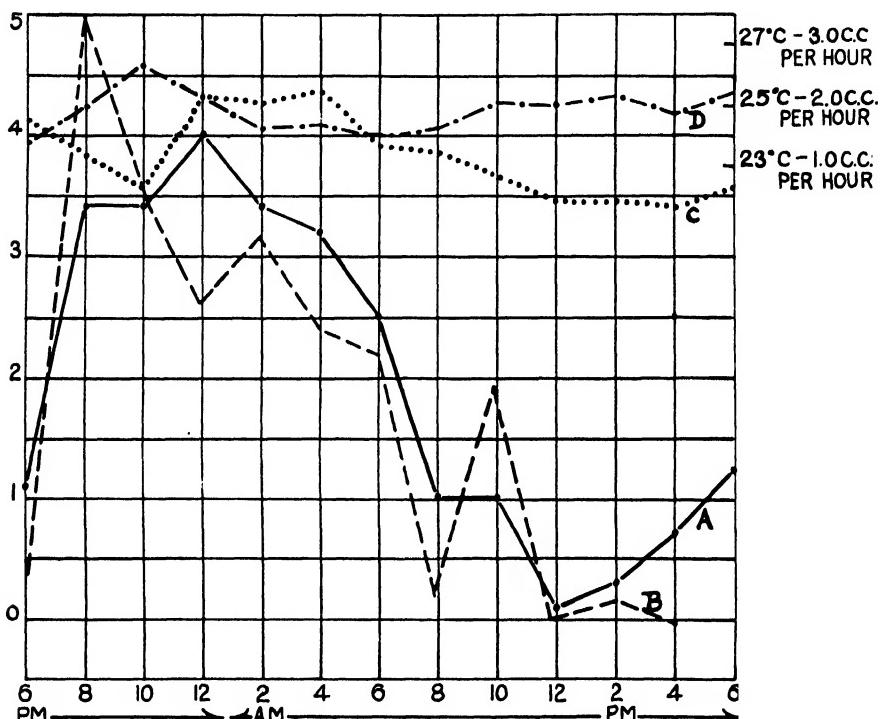


FIG. 7. Summary of periodic nocturnal activity in *Boletotherus cornutus* for four separate twenty-four hour periods in total darkness and practically constant air temperature and rate of evaporation. A = adult beetles collected in the forest; B = beetles raised from larval stage in laboratory in continual darkness; C = Rate of evaporation in c.c. per hour; D = Cabinet air temperature in ° C.

It must be concluded, therefore, that our nocturnal forest animals are of at least two types, one (*Parcoblatta pennsylvanica*) which is normally nocturnal but in which the activity is more or less easily modified by the environmental factor complex; the other (*Boletotherus cornutus*) in which the nocturnal activity is so deeply seated that it may be spoken of as nocturnal periodicity, *viz.* a rhythm in the strict sense.

DISCUSSION

It is to be expected that many crepuscular and nocturnal animals are adjusted to the nocturnal complex of operating factors. In this connection we may mention the light and dark adaptation in the eyes of decapod crustaceans (Herrick, '09; Welsh, '30 a, b; Bennett, '32 a, b); in the eyes of insects (Bugnion and Popoff, '14); the flashing of many species of fireflies in nocturnal mating (Mast, '12); the sensory adjustment of vertebrates (Crawford, '31).

Previous work (Johnson, '26; Rau, '29; Park, *et al.*, '31) led us to believe that the activities of many such nocturnal forms were modifiable by this factor complex, and the data on *Parcoblatta pennsylvanica* confirms this view.

However, the data on *Boletotherus cornutus* does not, and we must admit the possibility of at least two types of nocturnal activity. One in which the activity is readily modifiable experimentally, and another in which the activity sequence is so firmly entrenched that it tends to recur under constant laboratory conditions.

Are these two forms of activity distinct qualitatively, or are they quantitatively related? From the present data on these two species, it would appear that the types are basically distinct, but here the greatest caution must be exercised. It is possible that longer periods of controlled conditions would break down the sequence in *Boletotherus*, but here fatigue, hunger or other adverse physiological states would enter in, and further, such experiments would be so far from the natural environment of the animals that conclusions would be insecure. On the other hand, to attack this point a group of *Boletotherus cornutus* was obtained in October, 1931 from a different locality (Urbana, Illinois) and the beetles kept in the laboratory and fed upon gathered fungi for three months. After this prolonged exposure to relatively constant temperature and humidity, and irregular intervals and amounts of illumination, the experiments were repeated and 75 per cent of the animals still gave the night-active, day-inactive sequence under constant darkness, temperature and humidity. Twenty-five per cent were visibly slower in their movements, and their activity was irregular and unconvincing. Such a deep-seated cycle of activity as is indicated for this species would appear to be strictly periodic.

But can *Parcoblatta pennsylvanica* be termed periodic in the same sense? We think not. In the field it acts as though it were periodically active at night, but under controlled conditions with light absent, activity continues maximally until fatigue sets in. If this nocturnal species is periodic it is because the environment is periodic and the term "periodicity" used here is not identical in context with the rhythm of *Boletotherus*. Rau ('29, pp. 146-152; '32) has criticised the loose usage of the periodicity concept, and we believe justly so.

However, periodism in *Boletotherus* has been paralleled by other apparently deep-seated rhythms. Many crustacea are nocturnal, e.g. *Homarus*

(Herrick, '09), *Cambarus* (Newcombe, '29) and in the latter genus Bennett ('32b) found periodic migration of proximal retinal pigment in crayfish in total darkness, and Welsh ('30a) found periodic migration of distal pigment cells in the eyes of two Cuban shrimps (*Macrobrachium*) under constant illumination.

A few more authenticated cases of nocturnal periodicity in the absence of the apparently limiting stimulus are known and Welsh ('30a) has reviewed literature upon this point. Clearly much work remains to be done. Whether or not this or that species is nocturnally periodic in its activities must be discovered through experimentation on this isolated point. Thus the present status of information concerning the fireflies is unsound. Mast ('12) thought *Photinus pyralis* to be truly periodic in its activity, but Rau ('32) thinks the same species shows "adaptive behavior" to its periodic environment. Allard thinks light intensity, periodicity and temperature important in the same species ('31) and in the evening activity of the tree-cricket (*Oecanthus niveus*) ('30). Again, as early as 1893, Schwarz noted correlation between time of flight and onset of darkness in the ubiquitous May-beetle (*Phyllophaga*), and its nocturnal habits have been observed by many (Forbes, '07, '16; Davis, '16; Sanders and Fracker, '16) and yet the nocturnal activity of these common animals is not certainly known to be truly periodic in the strict sense.

Rau ('29), in a thorough study of sex behavior in four saturniid moths, found that each species had a normal period of nocturnal activity and thought light intensity to be highly important. Finding the response of *Platysamia cynthia* deeper seated than that of *Samia cecropia*, Rau concluded that the former was the older phylogenetically of the two. Data in the present report do not convince us of such a phylogensis, viz. by this reasoning *Boletotherus* would be held more ancient than the cockroach, *Parcoblatta*. Such a view is not necessarily incorrect, but palaeontological evidence on the general point, as well as their morphology is not in agreement with such an assumption.

SUMMARY

The forest cockroach, *Parcoblatta pennsylvanica*, and eight species of beetles distributed through three families were found to be active at night and inactive during the day under relatively normal fluctuations of the factor complex.

In total darkness, with temperature and evaporation rate constant, *Parcoblatta* tended to give maximal activity until apparently fatigued.

Under the same experimental conditions, however, the forest mycetocole, *Boletotherus cornutus* continued to exhibit its normal night activity and day inactivity. Such behavior is considered a strict periodicity of activity. Adults were reared from the larval stage in complete darkness, and other adults were gathered direct from forest fungi, but both groups gave the same form of nocturnal rhythm.

The significance of these two types of nocturnal activity is discussed with respect to current views on periodicity but conclusions reserved pending further accumulation of data.

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THE TENSION ZONE BETWEEN THE GRAMA GRASS AND PIÑON-JUNIPER ASSOCIATIONS IN NORTHEASTERN NEW MEXICO

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The immediate region in which these investigations have been carried on is the vicinity of Las Vegas, New Mexico. Westward from the area studied, the foothills, and then the mountains of the Sangre de Cristo range of the Rockies rise rapidly. Toward the east an extensive plateau and mesa land extends many miles, merging with the Great Plains. While altitudes vary markedly even in comparatively short distances, most of the tension zone studied lies between the altitudes of 6400 and 7000 feet above the sea.

The piñon-juniper association is the scrubby outreach of the forests that extend down from the mountains into the grasslands of the adjacent plains, at its outer margin interrupting them here and there, forming open stands of dwarf woodland. At an altitude just above the piñon-juniper association and merging with it at its upper margin in the mountains, is the forest of the western yellow pine (*Pinus ponderosa* var. *scopulorum* Engelm.).

Usually the piñons and junipers grow on rocky ridges and especially on the dissected edges of mesas (fig. 1). Not infrequently grasslands are on the

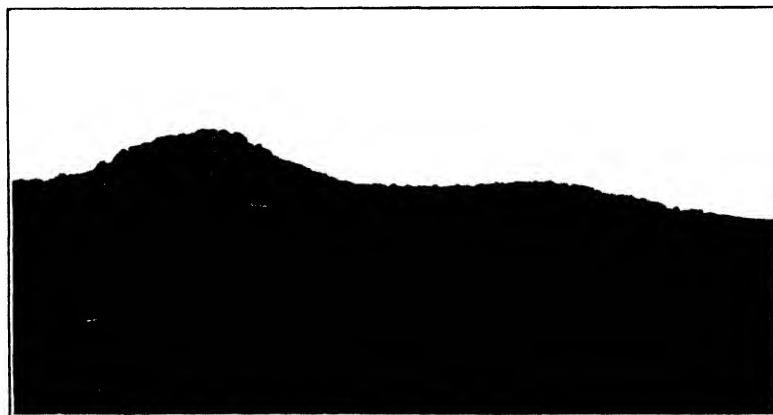


FIG. 1. Piñons and junipers on rocky edge of mesa. Grama grass in foreground. Note young trees becoming established on hillside below mature trees.

more nearly level areas at the foot of a mesa and on its top, with a zone of piñons and junipers occupying the rocky ledges at intermediate heights. This peculiar distribution raises the question of the underlying causes. Local conditions suggest such possible explanations as differences in types of soil, of

geological formations, of soil moisture, of rainfall, or of some peculiar manner of seed dispersal.

THE ASSOCIATIONS

In the grass association the ground cover consists chiefly of species of grama grass, *Bouteloua gracilis* Lag. and *B. curtipendula* (Michx.) Torr., and of buffalo grass *Bulbilis dactyloides* (Nutt.) Raf. With these are mixed smaller numbers of some other grasses, especially *Hilaria jamesii* (Torr.) Benth., and such other plants as *Yucca glauca* Nutt., *Malvastrum coccineum* (Pursh.) Gray, *Gaura neo-mexicana* Wooton, *Ambrosia psilostachya* D C., *Actinella simplex* A. Nels., and *Aster ericaefolius* Rothrock. A characteristic area in the grassland that was studied in detail had less than .4 per cent of bare ground.

The piñon-juniper association is made up of clumps of Piñon, *Pinus edulis* Engelm., and juniper, *Juniperus monosperma* Engelm. In some places, especially in higher, more xeric localities, and often extending high into the mountains there are extensive thickets of scrub oak *Quercus undulata* Torr. This species, however, comes only occasionally into the tension zone studied here. Sometimes individuals or small clumps of *Rhus trilobata* Nutt., *Fallugia paradoxa* (Don.) Endlich., and *Opuntia arborescens* Engelm. grow associated with the piñons and junipers.

The ground cover in the open spaces is made up largely of the species characteristic of the grasslands, with the addition of some three-awned grass *Aristida longiseta* Steud. However, the stands are decidedly sparse. Areas studied in detail showed from 25 per cent to 33 per cent of bare ground (fig. 2). Other areas that were only estimated varied from about 10 per cent to 95 per cent of exposed soil.



FIG. 2. Rocky soil with poor stand of grass. Characteristic of conditions in piñon-juniper association.

The types of soil on which the piñon-juniper association occurs differ very widely from each other, both as to character and as to geological origin. Occasionally this association is found thriving in fine, compact adobe soils, but usually it occurs in rocky places. The studies reported here were made chiefly on Greenhorn limestone, which belongs to the upper Cretaceous, and on Dakota sandstone of the lower Cretaceous (Darton, 1928). Some additional observations were made on an extensive bed of igneous gravels and boulders that had the appearance of a glacial deposit. Because of the great diversity of soil types on which the piñon-juniper association thrives the observer soon becomes convinced that the limiting factors are not primarily those of soil or geological formation.

INVESTIGATION

During the growing season of 1931 stations were kept for detail study about two miles in a southeasterly direction from Las Vegas. These stations were in open, unfenced range land on which only occasional winter grazing occurs. The most valuable data were obtained from a station in the grassland a short distance from the foot of the Las Vegas mesa and from one among the piñons and junipers on the rocky margin of the mesa. Records were kept of rainfall, soil moisture, and of evaporation rates from Livingston white, cylindrical atmometers run in duplicate. Reference to fig. 8 indicates at once that the slight differences in rainfall in the grassland and the scrub are not sufficient in themselves to account for the differences in vegetation in the two stations. However, the question remained as to whether or not there might be a significant difference in the water-supplying power of the soils in the two associations. Tests were made to determine this point.

SOIL MOISTURE

TABLE I. *Soil moisture records 24 hours after .75 inch of rainfall. Expressed in percentage of dry weight of soil*

Source	Non-available Water ¹	Total Water	Available Water
15-30 cm. deep Piñon-juniper association	13.7	22.5	8.8
30-45 cm. deep Same location	13.6	15.3	1.7
15-30 cm. deep Grassland	12.0	14.75	2.75

¹ Determined by permanent wilting of Milo maize seedlings in each type of soil. Averages from four to eight tests for each soil. This set of soils derived from Greenhorn limestone.

Table I is the record of one set of these tests. Other experiments carried on at different times in the year, but under comparable conditions, show these results to be reliable and representative of conditions during the rainy period

in summer. Examination of this table shows that even such a considerable rain as .75 inch affects soil moisture comparatively little below the upper foot (30 cm.) of soil, and that in the fine adobe soil where the grass was growing, most of the moisture remained in the upper 15 cm. of soil.

These differences of soil moisture lead to a consideration of the relation of available water to the positions of the roots in the soil.

ROOT SYSTEMS

The roots of most of the grasses occupy the first 30 or 40 cm. of soil. Occasionally a few penetrate to greater depths. With the main mass of grass roots limited to the first 30 cm. it appears that they penetrate to near the greatest depth to which ordinary rains sink, thus having access to practically all of the available soil water. In contrast with these shallow fibrous grass roots, the root systems of both piñons and junipers are quite generalized, readily adapting themselves to their surroundings. Except in places where rocks interfere greatly, the roots take two definite positions. One set extends in a horizontal direction at a distance from the surface of the soil of about 15 cm. to 30 or 40 cm., thus being in direct competition with the roots of grasses. In contrast with these horizontal roots, the tap roots, vertical laterals, or both, extend directly downward until they reach a rock bed, thence spreading out near its surface (figs. 3 and 4). These vertical roots have practically no competition for moisture that is in the deeper layers of soil.

TABLE 2. *Soil moisture records following a rainless period, expressed in percentage of dry weight of soil. Soil derived from Dakota sandstone*

Source	Non-available Water	Total Water	Available Water
15-30 cm. deep Piñon-juniper association	7.4	5.0	— 2.4
1 m. deep Same location	13.2	10.8	— 2.4
3 m. deep Among roots on top of sandstone	7.75	10.22	2.47

Table 2 shows the moisture conditions as they occurred during a rainless period. During the rainy season the surface soil is much like that in the piñon-juniper association recorded in table 1. It is a notable fact that the surface soil, during the dry period, may have a water content that falls considerably below the wilting coefficient for Milo maize, while at the same time the soil near the stone stratum, reached by the deeper roots, has a considerable amount of available water.

In order to test the relative efficiency of the horizontal and vertical parts of the root systems under field conditions, the taproots of five young junipers and 5 piñons were severed in late autumn of 1930, leaving all laterals uninjured. At the same time all laterals were cut of an equal number of young trees, leav-



FIG. 3. Juniper roots, showing that some are horizontal near surface of soil and that all others are vertical.

ing taproots only. All were given some mechanical support to prevent damage by the wind. At the end of the growing season of 1931 these ten trees were examined. All were found to be alive and to have grown during the year, thus showing that either set of roots seems adequate to supply water to the plant in years of normal rainfall, as this has been.

Another approach was made to the question of the relative amount of absorption by the different roots. A considerable number of roots were cut and introduced into bottles of water. Readings were taken and records kept



FIG. 4. Juniper roots. The vertical ones have reached sandstone layer and are extending horizontally in moist soil just above.

in the same manner as with atmometers. In all cases some water was taken in by the roots throughout the period of the experiment, which lasted from six to 16 weeks. Some roots soon seemed to give unreliable results. Data from these have been set aside for the present until additional work can be done. However, two junipers gave such striking results that the records are given in figures 5 and 6 along with the corrected readings of nearby atmometers.

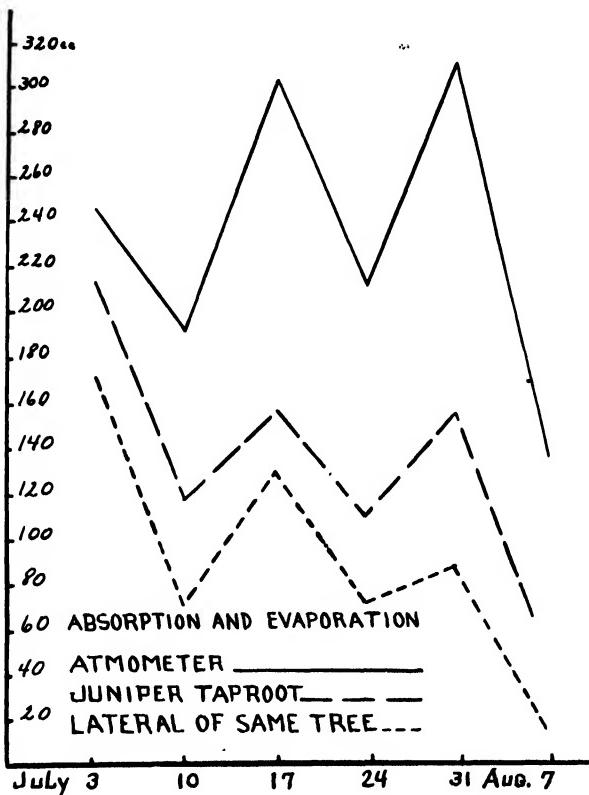


FIG. 5. Graphic comparison of records of corrected atmometers with the water losses from tap root and horizontal roots of young juniper.

The largest of these roots required a half-gallon fruit jar both because of the large diameter of the root and because of the considerable amounts of water taken up (fig. 7). Referring to figure 5 it is clear that both horizontal and vertical roots are active as absorbing organs and that during the growing season the rates of absorption by cut roots in free water very closely parallel the evaporation from atmometers. The one root from which records were kept until October (fig. 6) showed a marked decline in absorption toward the end of the season even when atmometer readings showed no great change. Plans are being made to try to refine this type of experiment in the near future in the hope of making it still more useful and reliable.

EVAPORATION AND RAINFALL

Figure 8 gives in graphic form the weekly records of evaporation from standardized white, cylindrical atmometers in the grassland and piñon-juniper associations. These records were taken in duplicate. In all cases the duplicate readings were quite in agreement. The figures used in plotting the evaporation curves are the average of the corrected atmometer readings for the station in question.

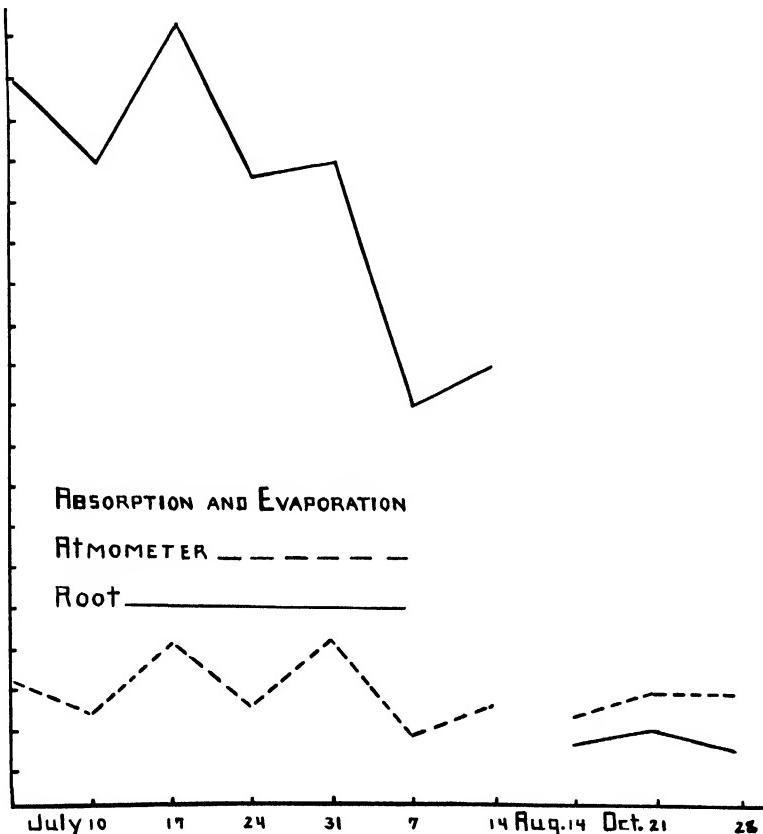


FIG. 6. Graphic comparison of corrected atmometer readings with intake of a large horizontal root of juniper. Note the marked reduction in activity of root in autumn.

The two stations recorded here were about 30 rods apart and the piñon-juniper station is estimated to be about 200 feet higher than the grassland station.

From the middle of June until the first of July enforced irregularity in taking readings made these useless, therefore they are omitted for this period. It was impossible to get atmometer records earlier in the season than those given, because of frequent frosts.

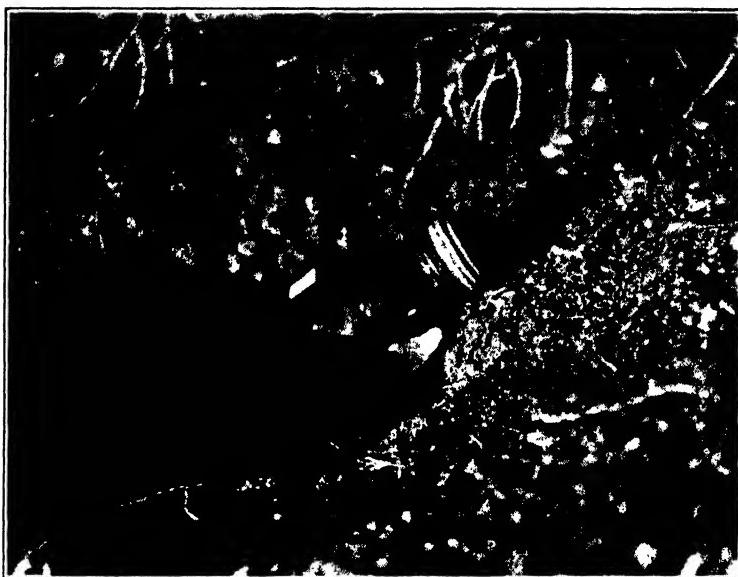


FIG. 7. Root with its water supply which gave data shown in fig. 6.

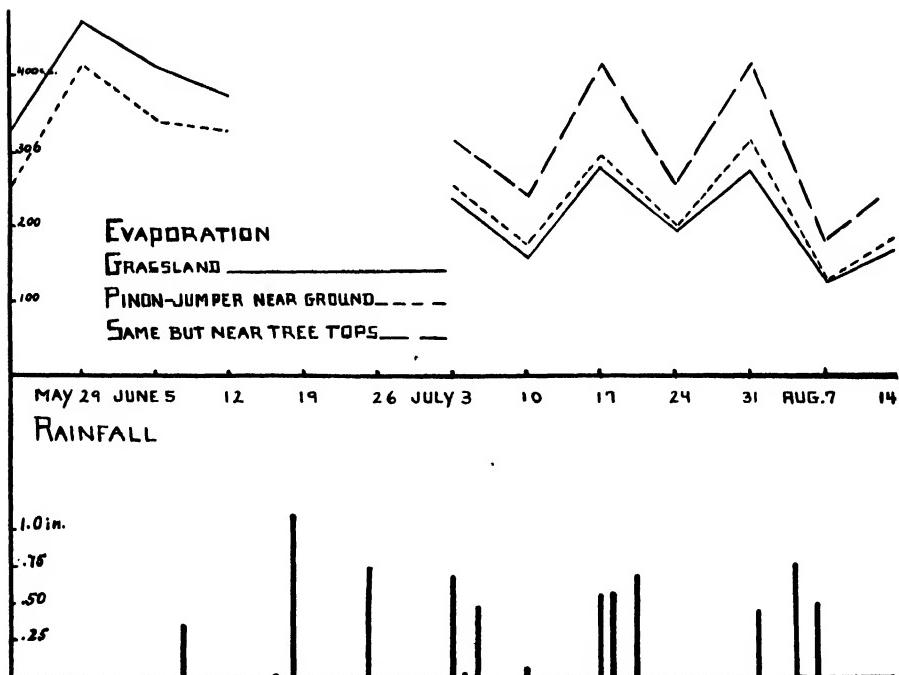


FIG. 8. Graphic comparison of evaporation and rainfall records.

A comparison of the evaporation rates in the grassland with those of the scrub shows that they are quite similar at the same distance from the ground. This means that the young trees have about the same conditions of evaporation to meet as the grasses. The older trees have a considerably higher evaporation rate at the level of their tops.

The rainfall that is recorded here covers most of the period of the rather indefinite rainy season using the records taken in the grassland (fig. 8). Comparison of the rainfall and evaporation records shows the expected relation between the two, evaporation running high at times of reduced rainfall and low following the heavier rains.

TEMPERATURES

TABLE 3. *Temperatures. From Weather Bureau records*

Week ending May				June				July					
8	15	22	29	5	12	19	26	3	10	17	24	31	
Mean temp. for week	52	68	55	62	63	63	66	70	68	65	70	69	69
Highest maximum	78	80	81	84	83	85	88	89	84	88	90	90	89
Lowest minimum	32	30	32	40	39	41	46	50	55	45	51	42	53
August				September				October					
	7	14	21	28	4	11	18	25	2	9	16	23	30
Mean temp. for week	69	66	63	66	66	67	66	60	61	55	52	52	52
Highest maximum	87	85	81	88	85	86	82	76	83	77	76	78	74
Lowest minimum	54	46	46	45	46	48	51	37	41	37	26	30	23

Table 3 records the weekly mean temperatures calculated from the sums of daily means. In addition, the highest maximum and the lowest minimum of each week is recorded to give some clue to the fluctuations to which the plants are subjected. These data are taken from the records of the United States weather station on the campus of the New Mexico Normal University about two miles distant from the stations at which all other records in these studies were taken. The altitude of the weather station is about the same as that of the field stations.

Comparison of figure 8 with table 3 shows that the highest temperatures of the year were practically coincident with the rainy season. The combination of warmth and moisture makes this the period of most active growth.

SEED DISPERSAL

An understanding of the seed dispersal of the piñons and junipers is necessary to a proper interpretation of this tension zone. Obviously the final

criterion of successful dissemination is the establishment of healthy seedlings in territory already occupied by the species, or in new areas. With this idea as a basis, a careful count was made of a representative area of 620 sq. m. Even the casual observer will note that one seldom finds young woody plants in the piñon-juniper association that are not growing protected to some degree by older woody plants of the same or another species. Table 4 illustrates this fact by actual count. This is in direct contrast with the reproduction of the western yellow pine as reported by Pearson ('30), but corresponds rather closely with the type of distribution of various shrubs described by Shreve ('31) in Arizona.

TABLE 4. *A tabulation of all adult and young woody plants on 620 sq. m. of area in the piñon-juniper association*

Species of Adults	Total Adults	Adults Harbor-ing No Seedlings	Adults Harbor-ing Seedlings	Species of Their Nurse Trees			Total Young
				<i>Juniperus monosperma</i>	<i>Pinus edulis</i>	<i>Opuntia arborescens</i>	
<i>Juniperus monosperma</i>	38	13	25	12	28	10	50
<i>Pinus edulis</i>	42	23	19	23	18	10	51
<i>Opuntia arborescens</i>	25	24	1	0	0	1	1
Totals	105	60	45	35	46	21	102

Table 4 also makes clear the fact that the seedlings are often not of the same species as their "nurse" plants. This points to some type of transfer of the seeds from the parent trees to a position under other trees. While it is impossible to tabulate results, the observer has not far to look for the active agent. Under many of the adult trees there are numerous holes, runs, and other evidences of the presence of small animals, presumably rodents. In the autumn, when the seeds are ripe, considerable piles of fragments of seeds and fruits of several kinds may be found under the sheltering trees and under rock ledges, but not in the open. The commonest of the species to be represented in these refuse piles are piñon, juniper, cocklebur (*Xanthium*) and various species of cactus. While close examination does not disclose any well-filled seeds in these collections, it appears probable that occasional seedlings grow from seeds that have been overlooked.

Not only do the mammals carry the seeds of these species but it appears that birds also take an active part in disseminating the juniper. Jays, especially, can be observed eating large numbers of the berries. The seeds of the juniper are very resistant and doubtless pass unharmed through the digestive system, being dropped in distant places. Such seeds would have little chance of growth if deposited in a close stand of grass. Even if the seeds were to reach the soil and if they were to germinate, the seedlings would have

to compete for moisture with the extremely efficient root systems of the grasses, thus greatly reducing chances of survival. However, the chances of successful growth of the seedling trees would be greatly increased if they happened to be in unoccupied soil. This may help to explain the presence of the junipers in rocky places and in other areas not well covered with grass. While it is at present impossible to have complete proof of this hypothesis, no facts that have been observed in any way disagree with it. On the other hand, many observations, as well as much of the experimental work, strengthen the theory. The juniper is the pioneer member of the scrub association, often extending its range as an occasional isolated shrub for some miles beyond the nearest general adult population of the species. The facts that birds eat the berries, that the pioneer individuals of juniper are almost always in places where grasses do not form a close stand, and that they often establish themselves too far from parent trees to be transferred by any other known means than birds, all lend strength to the idea that the bird is one of the very active agents of transfer of this species.

In contrast, the piñon has not been found far from possible parental individuals. This may be explained by the fact that the testa of this species is fragile, permitting the destruction of seeds that are swallowed by birds. Therefore the active agents in dissemination must be such as carry the seeds unharmed for comparatively short distances. Small mammals seem to be the most probable of these possible agents.

Aside from the two living agencies it is quite obvious that gravity plays a considerable part in scattering the seeds of both of these species when they are growing on hillsides. On level ground one seldom finds a seedling in an open space. However, on hillsides, considerable numbers may establish themselves in open spaces well below the parent trees. This shows that shade or other protection is not necessary to the growth of the seedlings, thus indicating that dissemination is the essential factor in the peculiar distribution of these species. On hillsides below trees, piñon cones and juniper berries may sometimes be found in considerable piles where they have rolled or have been washed.

Taking these various facts into consideration, it seems probable that the piñon-juniper association owes its ability to establish itself in rocky places to the fact that in these places the grasses do not form close stands; that when once established the piñons are transferred for comparatively short distances by the activities of burrowing mammals, while the junipers may be carried in the same way, or for greater distances by birds; and that in either case gravity tends to introduce these species into unoccupied spaces below the adults on hillsides. These conclusions are in entire accord with those of Cottle ('31) from his work in Texas, that the xeric grasses are the true dominants and that the woody plants can enter only in places where rocks, or in his locality, heavy grazing, prevent the full expression of the grasslands.

SUMMARY

The piñon-juniper association occupies an intermediate position between the montane forests and the short-grass plains, appearing most often in rocky places such as the edges of mesas. The juniper is found to be the pioneer of the two species, followed by piñon and occasionally other shrubby plants.

Studies are reported of soils, root systems, rainfall, evaporation rates, temperature, and seed dispersal. Soils in which the piñon-juniper association thrives, vary from fine adobe to outcrops of limestone, sandstone, and igneous gravels. The grasses are always poorly developed in the woodland soils. The combined effects of the condition of the stand of grasses and the efficiency of the agents of dissemination appear to be responsible for the location of the woody plants. Soil character and geological formation are only indirectly important as they control the growth of grasses.

Roots of the piñons and junipers assume both horizontal and vertical positions in any soil they can penetrate. Both sets of roots are found to be capable of active absorption. In rocks lying horizontally, the taproots develop very little, being replaced by laterals that follow the seams in the rocks. Grass roots are mostly in the first foot of soil in direct competition with the horizontal roots of the trees and with all of the roots of tree seedlings. This is probably a principal reason why the woody plants fail to establish themselves in close stands of grass.

Differences in rainfall are too slight and fluctuating to be responsible for the differences in vegetation. Rains seldom affect soil moisture below the roots of grasses and the horizontal roots of the trees. The vertical roots of trees may reach a continuous supply of moisture that follows the deep rock strata.

Woody plants are found to grow in clumps well separated from each other. On level ground the seedlings practically never develop except near shelters of some kind. On hillsides, on the other hand, they establish themselves in open places below parent trees. This proves that their usual position with older trees is not an obligate shade relation. Seeds dropped by birds and buried by rodents explain the presence of most of the seedlings under the adults and the consequent grouping into clumps.

The writer is glad to acknowledge his thanks to Prof. J. M. Greenman of the Missouri Botanical Garden for identifying certain species, and especially to the trustees of The Elizabeth Thompson Science Fund for funds with which to purchase the greater part of the equipment used in this investigation.

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THE INFLUENCE OF TWO BURROWING RODENTS, *DIPO-DOMYS SPECTABILIS SPECTABILIS* (KANGAROO RAT)
AND *NEOTOMA ALBICULA ALBICULA* (PACK RAT),
ON DESERT SOILS IN ARIZONA. II PHYSICAL
EFFECTS

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INTRODUCTION

The importance of animals in soil formation has long been recognized, but there is little data to show quantitatively, the changes that animals bring about. In another article Greene and Reynard ('32) have shown that both the Kangaroo rat and the Pack rat produce significant chemical changes in soils. The purpose of this paper is to show the physical changes which these animals produce.

EXPERIMENTAL METHODS

The soil samples were secured from the Santa Rita Range Reserve, a grazing substation of the Southwestern Forest and Range Experiment Station, United States Forest Service. This substation is located at the northwest base of the Santa Rita mountains, approximately 35 miles south of Tucson. The area of this Reserve is approximately 50,000 acres. Taylor ('30) has estimated the total rodent population at 2,000,000, of which about 500,000 are Wood rats and 100,000 are Kangaroo rats.

The system of sampling was the same as that described in the previous article (Green and Reynard, '32). Composite samples were taken at various depths, and check samples were taken from unworked soil some distance from the burrows.

The samples were air dried, and passed through a 20 mesh sieve. The alkaline salt content was determined on a water extract of one fraction, using a method similar to that described by Hibbard ('28). Only the total salt content is reported in the tables.

The water holding capacity was determined on another sample. The method used was that of Hilgard ('11). The moisture equivalent determination was made, using the method of Briggs and McLane ('07).

In order to determine what effects had been produced in the distribution of the various soil separates, a mechanical analysis was made, using the method of Bouyoucos ('30). Although this method has been criticized by several soil scientists, it has given fairly satisfactory results in this laboratory,

and the authors believe that it is sufficiently accurate for this study, where relative, rather than absolute variations are desired.

RESULTS

The results of these determinations are given in the following tables. The figures which are in italics and which are underscored are the results of the check samples.

DISCUSSION

An examination of the tables shows that in every case, there has been an increase in the soluble salt content of the soil, due to the activities of these animals. These increases are not as great, however, as some reported in another article (Green and Reynard, '32). Hence, any changes produced are probably chiefly physical (due to burrowing and tunnelling) and are not caused by the addition of organic matter (food storage).

The water holding capacity and the moisture equivalent determinations show that the soil has been appreciably changed, especially by the Kangaroo rat. At the top of the burrow the water holding capacity and moisture equivalent are greater than the surface check sample. This is due to the fact that the clay and finer sized soil particles have been brought to the surface, thereby increasing the values for these soil constants. Equally significant is the fact that in burrow No. 4, the values at depths of 10 and 16 inches are less than those of the check samples which were taken at the same depths. The heavier soil had been carried to the surface, but there was a larger percentage of coarser particles which were either never carried out of the burrow, or which had been transported back, either by gravity or by the animals. The mechanical analyses show that at — 10 and — 16 inches, the samples from the burrows contain a larger percentage of sand and a smaller percentage of clay than the check samples.

The changes produced in Burrow No. 5 are not as pronounced as those in Burrow No. 4, because the subsoil was sandy. The texture of the soil at the top of the burrow has been altered somewhat, as the figures for moisture equivalent and water holding capacity show. A mechanical analysis was not made of these samples, because of their sandy texture. The hydrometer method is not well suited for use on extremely heavy or extremely sandy soils.

Table III shows that the changes produced by the Pack rat are slight. This is to be expected, however, because it has a much simpler burrow system than the Kangaroo rat. The Pack rat burrow usually consists of a simple tunnel. The moisture equivalent and the water holding capacity of the sample from the burrow are slightly higher than those of the check sample. The percentage of sand is higher in the sample from the burrow, and the clay content is lower. This lack of agreement, however, falls almost within the limits of error of the methods used.

TABLE I. *Kangaroo Rat Burrow No. 4*

Lab. no.	Description	Total soluble salts, p.p.m.	Water holding capacity %	Moisture equivalent	Mechanical analysis		
					% Sand	% Silt	% Clay
17081-84	+2" Surface check.....	355	212	48.51	38.04	13.64	10.56
17082-5	-10"	896	268	51.61	71.80	15.18	23.21
17083-6	-16"	1177	172	61.16	71.73	19.19	23.52

TABLE II. *Kangaroo Rat Burrow No. 5*

17205-200	Top of burrow surface check..	379	190	36.43	29.53	8.88	6.45
17206	Ground level burrow.....	339	—	34.27	—	7.21	—
17207-201	-6"	462	274	35.82	32.80	9.36	7.32
17208-202	-12"	429	260	39.26	39.24	9.87	9.94
17209-203	-18"	269	185	40.68	41.25	10.41	10.25
17210-204	-24"	389	199	42.51	39.96	12.75	9.80

TABLE III. *Pack Rat Burrow*

18336	Burrow - 12"	833	—	34.02	8.30	—	8.38
18338-535	-16"	845	157	41.91	36.95	11.75	10.18

The results of the determinations of the moisture equivalent, water holding capacity and mechanical analysis are in fair agreement, although the two former agree better relatively, than they do with the results of the mechanical analysis. Actually, the moisture equivalent and the water holding capacity do not agree. It has been noted in this laboratory in connection with soil physics investigations, that the Hilgard method gives high values for the water holding capacity. When the moisture equivalent is calculated from the water holding capacity by use of the conventional formula: $M\text{ Eq} = (\text{WHC} - 21) \times 0.635$, the values are usually higher than those obtained experimentally; similarly, when the water holding capacity is calculated from the moisture equivalent by the formula: $\text{WHC} = (M\text{ Eq} \div 21) \times 1.57$, the values are usually lower than those obtained by the Hilgard method. There is, however, a relationship between these two values. The tables show that when there is an increase in the water holding capacity.

It has already been mentioned that Taylor ('30) estimates the Kangaroo rat population of the Santa Rita Range Reserve at 100,000, and the number of Pack rats at 500,000. There is usually only one animal per burrow, except at the breeding period. Some of the Kangaroo rat burrows have a diameter of 10 feet, and the total volume of a burrow may be 120 cubic feet or greater. When a soil has a heavy subsoil, which may be penetrated by the animals, the result will be an increase in the percentage of clay and silt on the surface of the burrow. This increase would be decidedly beneficial since there would be an increased moisture holding capacity, which also implies an increased holding power for plant nutrients. If a single animal can produce a burrow of an area of 80 square feet, 100,000 animals (at the same rate) could materially alter 8,000,000 square feet or approximately 184 acres. In the course of time, this figure might become significant.

CONCLUSIONS

1. The water holding capacity, moisture equivalent, and mechanical analysis has been determined for soil samples taken from the burrows of the Kangaroo rat (*Dipodomys spectabilis spectabilis*) and the Pack rat (*Neotoma albigena albigena*). These results have been compared with those of check samples which were taken a short distance from the burrows.
2. The Pack rat produced only slight physical changes in the soil.
3. The burrows of the Kangaroo rat were characterized by increased values for moisture equivalent and water holding capacity of the surface soil, and by a larger percentage of finer sized soil particles.
4. This "mixing" effect is very pronounced in soil having a heavy subsoil, and significant changes may be produced in the texture of the soil.
5. In the course of time, the physical and chemical changes produced by these animals will probably be beneficial rather than detrimental.

ACKNOWLEDGMENT

The authors wish to acknowledge their indebtedness to Mr. C. R. Reynard of Tucson, Arizona, who collected the soil samples, and kindly placed them at the authors' disposal.

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GROWTH AND REPRODUCTION OF YUCCA ELATA¹

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Yucca elata, Engelm., locally called soapweed, is a long lived perennial of the Liliaceae. Wooton and Standley ('15) describe the plant as follows: "Stems conspicuous in old plants, reaching a height of 3 to 4 meters, naked below, clothed with a tuft of leaves above; inflorescence a much branched panicle, leaves 10 mm. wide or less." Average plants in southern New Mexico vary from three to six feet in height, but specimens as tall as thirty feet have been observed. The slender, sharp pointed leaves forming the green



FIG. 1. *Yucca elata* plants in full bloom.

¹ The work upon which this paper is based was done on the Jornada Experimental Range, located about 50 miles north of the Mexican boundary near Las Cruces, New Mexico. It is a branch of the Southwestern Forest and Range Experiment Station, which is under the jurisdiction of the Forest Service, U. S. Department of Agriculture, and is conducted in cooperation with the University of Arizona, with headquarters at Tucson, Arizona.

crown may vary from 12 to 36 inches in length on different plants. Figure 1 shows some thrifty specimens in full bloom.

On the dry plains and mesas from western Texas, through southern New Mexico to southern Arizona, and into Mexico, scattered specimens of *Yucca elata* are found on every soil type, but it is particularly conspicuous on the more compact sandy soils, where its principal associated species are the grasses; *Bouteloua eriopoda*, *Sporobolus cryptandrus*, *S. flexuosus*, and *Aristida* spp. The stand may vary from a few to as many as 300 plants per acre in the *Bouteloua* association. As a rule, it is not abundant in the loose windblown soils of the *Prosopis* sand dune association, but occasionally occurs even there in stands nearly as dense as in the *Bouteloua* association.

Little detailed information is available concerning the fauna associated with *Yucca elata*, but field observations have shown that a great variety of species is found on or near the plant. Specific determinations of much of the material from studies now in progress have not yet been completed, but the following were either collected or observed in 1931:

Order	Species	Where found
INSECTA		
Homoptera	<i>Cicada</i> sp. }	Flowerstalks and leaves
	<i>Tibicen</i> sp. }	
	<i>Aphididae</i>	Flowers
Heteroptera	2 species	" and leaves
Lepidoptera	1 "	Leaves
Diptera	1 "	Flowers and leaves
Coleoptera	26 "	Various species on all parts of plant
Hymenoptera	<i>Formicoidea</i> —2 species	All parts of plant
	<i>Apoidea</i> — 1 "	Flowers
	<i>Vespoidea</i> — 3 "	"
REPTILIA		
Lacertilia	1 species	All parts of plant
Serpentes	1 "	Stem
MAMMALIA		
Rodentia	<i>Neotoma albigenula albigenula</i>	Stem and leaves
	<i>Lepus californicus texianus</i>	Nests at base of plant
	<i>Sylvilagus auduboni minor</i>	Feeds on leaves within reach
		Feeds on leaves within reach and inhabits deserted <i>Neotoma</i> burrows at base of plant.

VALUE OF YUCCA ELATA

Even in scattered stands, *Yucca elata* has a definite economic value. In the semi-desert southwest, every plant plays at least some part in bringing about soil stability and improvement. Since it is a very long lived perennial, it is one of the few plants which continually help protect the soil from both

wind and water erosion. The leafy crown and the thick stem intercept rainfall, and check its flow; the numerous lateral roots bind the soil, protecting it from washing or blowing away; and the old dead leaves and material added by the dead bodies of fauna associated with the plant improve the organic content of the adjacent soil enough to increase materially its water holding capacity. If the herbaceous vegetation on the range becomes badly depleted, the *Yucca* plants obstruct considerable soil during wind storms.

Yucca elata furnishes shade for livestock and has a certain value as forage, especially as emergency feed for cattle during prolonged drought periods. When other range feed is short during the winter or spring months, cattle take the green leaves. The sharp points of the leaves discourage grazing, but when forced to do so, cattle learn to chew the leaves from the stem out toward the sharp ends. Forsling ('19) states that: "In the fall of 1917, a herd of cattle in southern New Mexico was maintained for at least two months on a range where the green soapweed leaves furnished 50 per cent or more of the feed." The young leaves which start growth at the center of each leaf cluster in the spring are especially relished by cattle. The succulent flower stalks, and large flowers, also are quite palatable, and furnish considerable forage during May and June, when other vegetation usually is dormant.

Yucca elata was used extensively in southern New Mexico for supplemental feeding during drought from 1916 to 1919. Forsling ('19) reports from work done on the Jornada Experimental Range during this period, that *Yucca* plants were cut and chopped for ensilage, after the dead leaves were burned off. The stems are fibrous, but very pulpy, and he concluded that the feeding of chopped soapweed, with a supplemental ration of cottonseed meal or other similar concentrate, is a practicable means of maintaining range cattle during severe drought.

The large caudex of *Yucca elata*, called "amole," is saponaceous. It is used locally, and according to Dayton ('31), to some extent commercially for soap. The stem and leaves of the plant contain abundant fibers which are considered of potential economic value. The fibrous strands laid down by the growing point of the stem are much branched, and are continuous with those of the leaves. The stems make a very small annual addition of secondary fibers.

Wooton ('13) recommends *Yucca elata* as a hedge or windbreak because of its thick heads. However, he reports that because of its deep tap root, which often must be cut in excavating the plant, twenty-five per cent or more of the transplants usually are lost, depending somewhat upon the amount of water supplied at transplanting and during the first season.

GROWTH AND REPRODUCTION OF YUCCA ELATA

Because *Yucca elata* is an important range shrub, studies of its growth and reproduction were started on the Jornada Experimental Range in 1925. In that year, several plants were selected for study with various methods of

treatment; and in 1931, height measurements were made on the sprouts from plants cut for ensilage in 1915. Special studies of seedling growth and behavior also were made in 1931.

In November, 1925, two *Yucca* plants in an area protected from grazing were selected, and the growing point of each was measured for height above the soil surface. Leaf and flower stalk measurements also were made, and all measurements were repeated in October or November every year, including 1931. The two plants showed some individual variation in height growth each year, but taken together followed rather closely the precipitation for certain seasons of the year, as shown in table I. The data indicate that the greatest height growth is the result of high rainfall, well distributed throughout the nine months preceding the measurement in October. The direct effect of extreme rainfall during any one season of the year upon stem growth is not shown conclusively from the records available, although the effectiveness of summer rainfall is indicated. Furthermore, measurements made in 1926 showed that practically all of the stem growth that year was made during the summer.

TABLE I. *Precipitation by seasons and average annual growth of Yucca elata, 1925 to 1931*

Year	Precipitation				Average Height	
	Jan.-Feb.- Mar. Inches	Apr.-May- June Inches	July-Aug.- Sept. Inches	Oct.-Nov.- Dec. Inches	Total Inches	Growth of <i>Yucca</i> Inches
192536	1.00	3.76	1.81	6.93	
1926 2.19	3.13	7.89	4.40	17.61	1.12
192777	.08	6.41	.50	7.76	1.00
192872	1.21	3.62	3.95	9.50	.88
192979	2.19	7.55	1.92	12.45	1.00
1930 0.	.22	2.52	1.25	3.99	.50
1931 2.51	2.17	5.42			1.25

The average annual growth of the two plants during the six years was 0.06 inch. The maximum growth of a single plant in one year was 1.50 inches, while the minimum was 0.50 inch. Growth of as much as two inches has been measured on other plants during a year with exceptionally high rainfall. In order to obtain a more representative figure for the average annual growth of *Yucca elata*, 25 sprouts from plants which were cut down in the autumn of 1915, were measured in 1931. The highest was 31 inches, the shortest was 8 inches, with an average height of 16.08 inches. Since the plants were 15 years old, the average annual growth was 1.07 inches, which checks very closely with the growth of the two more mature plants measured from 1925 to 1931.

The leaves of *Yucca elata* grow more quickly, but are more short lived than the stem. The leaves remain green throughout the year, but grow very little during the winter. In the spring, usually in May or June, new leaves

in the center of the cluster start growth and lengthen during the summer and early fall. New leaves continue to appear in the center of the cluster during the summer. Leaf measurements made in 1926 show the rapidity with which the growth occurs. On July 27, several young leaves, which were measured and tagged, had an average length of 6.3 inches. On August 3, just one week later, they had an average length of 13.7 inches, an average growth of 7.4 inches, or slightly over an inch each day. On August 24, three weeks later, the same leaves averaged 14.8 inches in length, an increase of only 1.1 inches in 21 days. Thus, the main leaf elongation takes place within a very short time. Measurements to locate the region of growth in the leaves showed that it is almost entirely basal, with practically no measurable elongation of cells after they are over two inches from the stem. At first, the new leaves are vertical and are encased within the center of the cluster of more mature leaves. As each leaf grows, it becomes part of the protecting group for the still younger leaves, and as the stem grows, assumes an acute angle to the stem axis during its first season of growth. During its second year, it comes to a position at about 45 degrees to the stem axis, and by the third year, is either in a horizontal or slightly drooping position. Leaves on many plants begin to die after the third year, gradually point downward and eventually rest against the stem in a nearly vertical position. Some leaves remain alive for as many as five years, but most of them die after the third or fourth year. The dead leaves persist on the stem for many years, until they finally disintegrate and blow away, or are rubbed off by cattle. The fibers in the leaves, continuous with those in the stem, are responsible for this persistence.

Yucca elata reproduces mainly by vegetative means. Any treatment which destroys the growing point means the death of the mature stem, and usually results in the production of sprouts from the base of the plant. The accumulated dead leaves on the *Yucca* plants burn well, and often are fired by cowboys or travellers during cold weather to furnish a brief warming place, although lightning or accidental grass fires are responsible for the burning of many *Yuccas*. The fire usually goes clear to the top of the stem. Soon afterward the terminal leaf cluster dies and within one or two years the entire main stem rots away at the base and falls over. Occasionally, if the fire does not reach quite to the top, the growing point is not injured fatally, and the main stem continues to grow. If the stem is cut off, the plant dies back to the first sprout, which may be from 2 to 12 inches under the soil. The caudex of the plant is very persistent and if the first sprouts are killed by rodents or from some other cause, other sprouts come up the next year. Some actual cases of vegetative reproduction will illustrate the variation.

In 1925, a *Yucca* plant 38 inches high was cut off at 4 inches above the soil surface. In 1926, a sprout came up near the old stump and continued to grow through 1931, with no other sprouts appearing. Another plant, 52 inches high, was cut at the same time, and in the same way. In 1926, two sprouts appeared near its dead stump, but one of these died during the spring

of 1927 and the other during the spring of 1928. Both were damaged badly by rodents. In 1929, a third sprout came up but died the following spring. Then in 1931, two more sprouts appeared, and with the excellent rainfall of that year, developed exceptionally well. As many as five sprouts have been observed near the base of a dead stem. Sprouts often spring up even from the base of a living stem, and grow in a manner similar to the sprouts from cut or injured plants.

The growth rate of sprouts is much the same as that of more mature stems. Three sprouts measured annually from 1929 to 1931 had an average annual height growth of 0.96 inch. These sprouts started in 1926, but required three years to develop a stem high enough to measure. This growth for three years corresponds exactly with the growth rate found on two mature plants from 1925 to 1931, and very closely with the 1.07 inches per year found in 25 sprouts for 15 years. The maximum growth measured on a single sprout in one year was two inches, while the minimum was 0.50 inch. The growth of sprouts followed rainfall as closely as did the growth of mature plants shown in table I. Figure 2 shows a bisect of a *Yucca* burned in June, 1930,



FIG. 2. Partial bisect of a burned *Yucca elata*, showing caudex, dense lateral root system and new sprouts.

with its sprouts in October 1931, after two seasons of growth. The comparatively rapid growth of sprouts is due very largely to the well developed root systems, in the uppermost 18 inches of soil, of the mature plants which produce them. Cottle ('31) has shown that the caudex of *Yucca elata* ends

abruptly at the calcareous layer, and has poorly-branched main roots running outward to distances of 5 to 10 feet.

When winter and early spring rains are abundant, many *Yucca elata* plants on the range produce flower stalks. Table I shows that in 1926, and again in 1931, favorable rainfall occurred during the previous autumn, continuing through the winter and spring periods of the current year, and from 1925 to 1931, these two years were marked for the abundance of *Yucca* blooms. Every year, a few Yuccas flower, but it is only in the exceptionally favorable year that the majority of the plants bloom.

The flower stalks usually appear during May and June, and come into full bloom during late June and early July. Flower stalks occur sooner or later on nearly all plants taller than 15 inches, and have been found on plants only 6 inches high. Their development is very rapid as is shown by table II. These data show that during their most rapid growth, the two flower stalks observed increased an average of 2.52 inches per day. The height of flower stalks varies considerably on different plants and in different years; the shortest flower stalk observed was only ten inches high in 1928, while the longest was 96 inches high in 1931. The flower stalk grows up through the center of the leaf cluster, and is protected by the leaves during the first several inches of growth. The elongation is largely terminal, with approximately 63 per cent in the uppermost 4 inches of the stalk, 32 per cent in the second 4 inches, and only 5 per cent below the 8 inch zone, as determined by detailed observations made on two flower stalks in 1926.

TABLE II. *Weekly growth of two Yucca elata flower stalks, 1926*

Date of Observation	Plant No. 1 Total Height Inches	Plant No. 2 Total Height Inches
May 25	Start.....	0
June 1	18	Start
June 8	38	19
June 15	58	33
June 22	68	48
June 29	72	54
July 6	76	60

The flower stalk is surmounted by a great panicle of white or cream colored flowers arranged in much branched compound clusters, as shown in figure I. Very rarely, as reported by the senior author ('29), a case of phyllody occurs. The number of flowers produced on a single stalk varies from 75 to sometimes over 200. The flowers attract many insects, so that cross pollination should be accomplished, but the percentage of flowers which produce seed pods is low. In fact, many panicles of flowers produce no seeds at all, while the maximum observed production of seed pods from flowers is approximately 30 per cent. However, each seed pod contains 150 or more seeds, so that ample seeds are produced in years when high rainfall favors flower stalk production.

The seeds are light and are well disseminated by the wind when the pods open during the late summer and autumn. They usually have a high viability percentage, as shown by germination tests made from 1925 to 1931. Of nine random samples tested during those seven years, 5 had over 90 per cent germination, 3 were 50 per cent or over, and only one had no viable seeds. In one sample of one hundred seeds, 99 germinated.

Reproduction by seed is very limited because few seedlings become established, and their growth is extremely slow. In 1915, 75 one meter quadrats were established in *Bouteloua criopoda* associations on the Jornada and adjacent ranges for range management studies. The soils were suitable, and *Yucca elata* constituted at least 2 per cent of the stand in the types surrounding the quadrats, but on only 4 of the 75 were *Yucca* seedlings present, with only one on each quadrat. Only ten seedlings have been observed during 17 annual chartings of these study plots, and in 1931, only six living seedlings were recorded on a total of 170 quadrats. Occasional seedlings not on the quadrats have been noted.

The unusual feature is that none of the seedlings recorded grew enough to have a measurable stem height, even in 1931. Quadrat B-3 supported one seedling when it was established in June 1915. The seedling was charted on the quadrat every year, but in October 1931, sixteen and one-half years later, it had just 16 leaves with an average length of 7.5 inches, and its stem still was too short to measure above ground. A more striking case was found on quadrat B-2, which supported one *Yucca* seedling when it was established in June 1915. The seedling was charted every year until October 1922, when it could not be found on the quadrat, and was not mapped in the next two annual chartings. In October 1925, however, the seedling was found in the same location on the quadrat, and was charted each following year, including 1931, when it had 22 leaves with an average length of 8 inches.

The extremely slow growth of *Yucca elata* seedlings may be attributed partly to their comparatively limited root systems, as shown by the bisect in figure 3, the full significance of which is brought out by a comparison with figure 2, which shows the ample root system by which sprouts are supported.

Rodent damage is responsible in part for the slow development of *Yucca* seedlings and sprouts, and often of retarded growth in more mature plants. Wood rats (*Neotoma albicula albicula*) cut leaves from mature plants, and rabbits habitually cut off a few of the leaves of seedlings or sprouts within their reach. At times they cut all the leaves, and even the growing point so that the plant dies back and is forced to send up a new sprout to continue its life. This undoubtedly is what happened to the seedling on quadrat B-2, which was charted from 1915 to 1921, disappeared for three years, was charted again in 1925 and then continued to grow. The same situation is evident on the seedling shown in figure 3, which died back at least twice before the existing leaf cluster was produced. Rodent damage undoubtedly

causes the death of many sprouts. This conclusion is supported by the fact that late in the summer of 1930, there was a noticeable decrease in the rabbit population on the Jornada range, with the result that in 1931, little damage was recorded and practically every seedling and sprout observed made unusually good growth.

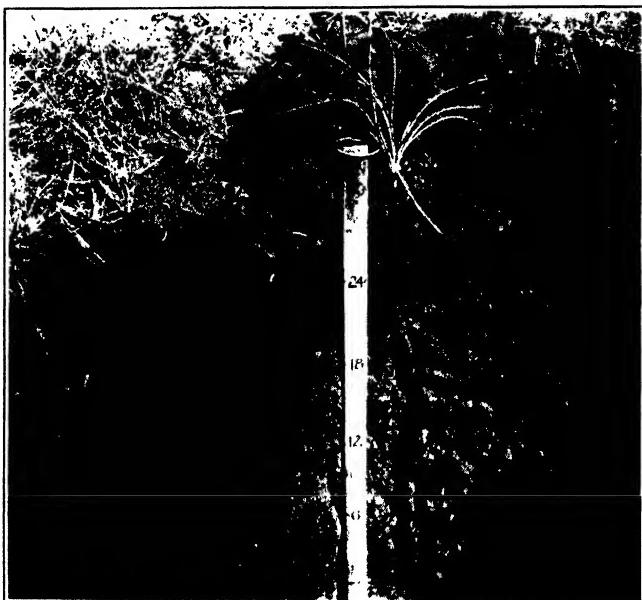


FIG. 3. Bisect of a *Yucca elata* seedling, showing the caudex ending at the hardpan, and sparse development of lateral roots.

MANAGEMENT OF *YUCCA ELATA*

On conservatively grazed range, supporting the *Bouteloua eriopoda* climax stage, *Yucca elata* has little importance as feed in most years, because it furnishes so small a proportion of the actual forage. However, because of its value as emergency feed during drought, both on the range and as ensilage, and its possible commercial use for fiber, a policy should be developed for the management of *Yucca*, in case further cutting should be undertaken in the future. Since the plant reproduces so prolifically by sprouts and so poorly by seed, it should not be necessary to leave any large plants for seed production, although it would be desirable to leave a few mature plants to furnish shade and protection from winds to live stock. According to Forsling ('19), it is not profitable to cut plants under 36 inches in height for feed, and since ordinarily more than 50 per cent of the plants are less than 36 inches, the cutting of stems above that height leaves enough plants to furnish reasonably effective protection from wind erosion. Further, if cutting is done only for emergency feed, the amount of feed furnished by flower stalks, blossoms, and

green leaves is not reduced materially. Selective cutting for emergency feed, then, would require a minimum cutting cycle of 15 years on a given area, and at least 20 years after the first two cuts, based on a growth rate of approximately one inch per year for both mature stems and sprouts.

Just what would be the most profitable minimum size for cutting to produce fiber can be determined only by study. The cutting cycle would depend upon the minimum size, the area of plants available for cutting, and annual requirement of the fiber factory. In any event, the probable cutting cycle would be similar to that necessary for emergency feed production.

SUMMARY

Yucca elata, a perennial shrub of the Liliaceae, occurs on the dry plains and mesas of southern New Mexico and adjacent parts of western Texas, southern Arizona and northern Mexico. Even in scattered stands, it is of value in reducing wind erosion, its flower stalks and flowers are eaten readily by cattle in late spring, and its green leaves furnish feed for cattle in dry springs when grass is scarce. *Yucca* plants were chopped for ensilage and were used extensively in southern New Mexico for supplemental feeding during drought from 1916 to 1919. The stems have abundant fibers which are of potential economic value, and the roots often are used for soap. In addition, the plant is a desirable ornamental, although its deep root system makes transplanting difficult. There is an abundance of fauna associated with the plant. Insects especially are numerous when it is in flower.

Measurements of mature *Yucca elata* plants show an average annual height growth of approximately one inch, and indicate that the amount of growth depends largely upon the rainfall, especially the summer seasonal. As much as two inches growth was observed in a favorable year, while the minimum growth observed was 0.50 inch in a dry year. The leaves grow rapidly from the center of the leaf cluster during the summer, but gradually droop during the second and third years of growth, and usually die at the end of the third or fourth season. The dead leaves persist close to the stem for many years.

Yucca elata reproduces both by seed and from sprouts. Although seed viability generally is good, few seedlings have been observed, and the data show that in 16 years, the seedlings on record grew very slowly, with no measurable stem development above ground. Any injury to the growing point of a *Yucca* usually kills it, the stem dies back, and sprouts come up from the base. The growth of sprouts is very similar to that of mature plants. Rodents cut the leaves of all plants to some extent, but rabbits especially are responsible for leaf cutting and resultant retarded growth of seedlings and sprouts.

On a basis of cutting no plants under 36 inches in height, the cutting of *Yucca elata* for ensilage should be on a minimum cycle of 15 years, while at least a 20 year cycle probably would be required after the first two cuttings.

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THE EFFECTS OF DEHYDRATION UPON THE HATCHABILITY OF *LIMAX FLAVUS* EGGS

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While one of us (E. B. C., '31) was investigating the action of ultra-violet rays on the embryos of *Limax flavus* Linnaeus, it was noticed that some batches of eggs were so dehydrated that they were wrinkled or had depressions in them. This condition prevailed if the eggs were laid in a dry or moderately damp receptacle. These eggs, however, would hatch if placed in a moist container.

Khalil ('22) found that *Planorbis corneus* were quite susceptible to drying, being killed in five hours when in a jelly-like mass. Adolph and Adolph ('25) placed *Lumbricus terrestris* in a 0.136 M solution of sodium chloride for twenty hours and found that the worms would recover after a 35 per cent loss in weight. Jackson ('26) also, working on *Lumbricus terrestris*, found that they would live, after losing 43 per cent of their original weight in four to five hours, when placed on dry filter paper. Jackson found that they would die if they lost 50 to 60 per cent of their weight.

Since the eggs of *Limax flavus* Linnaeus hatched after being dehydrated enough to show a definite depression, we decided to perform a series of experiments to determine the maximum loss in weight which the young would survive and still be able to hatch. The eggs are fastened together by means of a membrane and thus all are laid at once. The slugs do not move while laying; hence the eggs become superimposed and are able to retain their moisture for a longer period than single eggs. The eggs varied considerably in weight: the maximum being 97.49 milligrams and the minimum being 51.16 milligrams. The average weight for 1,200 eggs was found to be 78.71 milligrams. The eggs are elliptical in shape, the average diameter being about 0.5 centimeter and the average length being about 0.75 centimeter. They are covered with a rather tough membrane, which allows them to be moved on dry filter paper without being ruptured. A vitelline membrane surrounds the embryo, and this membrane is surrounded by a semi-fluid gelatinous mass, which resembles egg white. These experiments were conducted at room temperature (20 to 30° C.).

The slug eggs, containing embryos from one to twenty-two days old, were weighed and subjected to dehydration. The eggs were placed on clean dry filter paper, the drying process lasting from two to seven hours. The eggs were weighed at the end of definite periods and placed in Petri dishes on moist filter paper. The weights given in this paper are averages in all cases.

TABLE I. Data relating to hatchability of slug eggs which were dehydrated for definite periods

Age of eggs	Time until controls began to hatch	Average weight	Hatchability with reference to time dehydrated and to per cent loss in weight						Controls		
			4 hours dehydration			5 hours dehydration			6 hours dehydration		
			No. of eggs	Loss in weight	No. of young lived	No. of eggs	Loss in weight	No. of young lived	No. of eggs	Loss in weight	No. of young lived
days	days	m gm.	%	%	%	%	%	%	%	%	%
1	1	22	68.81	7	70.93	6	—	—	7	86.51	—
2	1	23	77.00	3	87.01	—	—	—	—	—	—
3	1	21	60.74	14	42.85	12	—	—	—	—	—
4	1	22	63.36	3	84.73	2	3	87.37	—	—	—
5	3	23	74.00	7	54.12	5	—	—	7	79.35	3
6	4	23	66.73	9	69.24	5	9	84.68	2	—	—
7	4	23	67.87	8	70.89	5	—	—	8	85.62	1
8	5	22	69.13	8	69.63	3	—	—	8	83.04	3
9	5	23	74.21	5	62.27	—	—	—	5	83.83	1
10	6	20	87.12	12	74.17	7	12	85.22	8	—	—
11	6	23	76.52	5	81.70	3	—	—	—	—	—
12	7	21	54.27	5	77.88	4	5	86.36	—	—	—
13	7	24	75.55	4	86.10	3	4	87.75	—	—	—
14	8	23	76.60	13	71.68	7	13	80.62	3	—	—
15	8	23	51.21	7	86.68	—	—	—	—	—	—
16	10	23	78.26	13	66.37	10	13	79.16	7	—	—
17	10	23	77.56	10	79.87	8	10	86.85	—	—	—
18	11	27	75.00	3	72.58	3	3	81.33	2	—	—
19	11	23	77.33	4	73.81	2	—	—	—	—	—
20	11	23	96.44	9	67.62	8	—	—	—	—	—
21	12	22	52.64	5	75.30	4	5	77.96	3	—	—

TABLE I. (*Continued*)
Hatchability with reference to time dehydrated and to
per cent loss in weight

Lot No.	Age of eggs	Time until controls began to hatch	Average weight	Controls									
				4 hours dehydration				5 hours dehydration				6 hours dehydration	
				No. of eggs	Loss in weight	No. of young eggs	No. lived	No. of eggs	Loss in weight	No. of young eggs	No. lived	No. of eggs	No. of young eggs lived
22	12	22	64.40	5	78.26	2	5	83.85	2	5	88.19	—	5
23	12	25	73.06	4	64.41	4	—	—	—	4	86.72	—	3
24	13	23	78.42	3	72.59	3	3	78.32	2	4	90.44	—	3
25	13	22	77.65	8	72.24	5	—	—	—	8	77.44	—	8
26	13	22	64.60	8	65.17	4	8	75.04	5	—	—	7	7
27	13	24	72.50	3	82.99	2	3	88.51	—	—	—	3	3
28	14	21	69.66	4	82.41	1	4	87.43	—	—	—	2	2
29	15	23	72.64	—	—	—	4	81.62	2	—	—	5	5
30	16	22	83.61	4	61.42	3	4	75.30	3	—	—	6	5
31	18	21	70.71	—	—	—	—	—	—	7	41.81	5	7
32	19	22	65.07	5	65.88	4	—	—	—	5	75.16	4	4
33	19	25	70.94	8	81.20	7	8	85.55	—	—	—	8	8
34	20	24	77.93	5	69.20	5	5	78.95	4	—	—	2	2
35	20	25	75.80	6	80.21	4	6	85.25	—	—	—	6	6
36	21	24	68.33	6	84.10	—	—	—	—	—	—	3	3
37	21	23	66.90	6	82.33	—	—	—	—	—	—	3	3
38	21	24	63.69	12	77.12	4	12	84.29	—	—	—	9	9
39	21	23	63.40	5	84.22	—	—	—	—	—	—	5	5
40	21	21	75.63	5	62.10	5	—	—	—	—	—	8	8
41	22	23	71.20	8	53.13	8	—	—	—	—	8 ^a	75.07	7

¹ One egg contained twin slugs.

^a These eggs were dehydrated for seven hours.

Table I shows the effects of dehydration for definite periods of time on the hatchability of slug eggs (the lots included in this table are given as examples).

From the data in table I it can be seen that the eggs which contained the younger embryos hatched after losing as much as 85 per cent of their weight, while the eggs which contained fully developed (full term) embryos failed to hatch after losing about 75 to 80 per cent of their weight. Several of lots 33 and 35 hatched after losing more than 80 per cent of their weights, but these were only about three-fourths matured at the time of dehydration. Several lots (nos. 5, 14, 25, 31, 40 and 41) were dehydrated during rainy periods, and they lost weight much slower than eggs which were treated in dry weather. The time of dehydration was not the main factor in the experiments, since four hours treatment was sufficient to kill the embryos in several lots (nos. 2, 15, 36, 37 and 39), while six hours did not kill all the embryos in several other lots (nos. 5, 8, 31 and 32).

Since the duration of the dehydration process did not seem to be the chief factor in preventing the eggs from hatching, we decided to dehydrate some eggs until a definite loss in weight had been reached for each egg. The time required to dehydrate to a given weight varied several minutes for eggs of the same batch; so this part of the data has been omitted. Table II contains the data on the dehydration of eggs (containing full term embryos) to a definite per cent loss in weight.

TABLE II. *Data relating to hatchability of slug eggs after they were dehydrated to definite weights*

Lot no.	Age of eggs	Time until controls began to hatch	Average weight	75% Loss in weight		77.5% Loss in weight		80% Loss in weight		Controls	
				No. of eggs	No. young lived	No. of eggs	No. young lived	No. of eggs	No. young lived	No. of eggs	No. young lived
1	22	22	62.75	—	—	—	—	2	—	3	3
2	20	23	59.23	3	3	3	2	—	—	5	5
3	20	20	53.92	9	7	3	—	—	—	17	17
4	19	19	84.42	3	1	5	1	5	—	4	4
5	23	23	84.20	8	6	—	—	5	—	5	5
6	20	20	87.49	4	4	—	—	—	—	2	2
7	19	19	68.73	—	—	5	1	5	—	4	4
8	20	20	65.91	—	—	—	—	3	—	4	4
9	19	19	51.16	—	—	—	—	2	—	1	1
10	20	23	87.65	—	—	—	—	4	—	1	1

None of the full term embryos lived after the eggs had lost 80 per cent of their weight. About one-fourth of the young lived from the eggs which lost 77.5 per cent of their original weight. The majority of the young lived from the eggs which lost 75 per cent of their weight.

In order to show that the young slugs were losing weight during the process of dehydration and that the loss was not entirely due to the decrease

in the weight of the jelly-like material of the eggs, the following control experiments were performed (normal embryos from the same lots as used in table II were employed): (a) after being dissected out of the eggs, the embryos were weighed as soon as possible; the average weight was found to be 20.27 milligrams, and (b) some of the eggs from the same batches were dried until they reached the average weight of the normal young slugs for that batch; then these slugs were dissected out and weighed, the average weight being 12.68 milligrams. These young slugs, after losing as much as 35 to 40 per cent of their body weights, lived. The eggs (containing full term embryos) which were dehydrated until they reached the weight of the normal young slugs always hatched, since this resulted in much less than 80 per cent loss in weight (the embryos in 51.16 milligram eggs equaled 35.18 per cent of the eggs, while the embryos in 93.66 milligram eggs equal 22.53 per cent of the eggs). From the data in table II one can see that the embryos would hatch and live after the eggs lost 75 to 77.5 per cent of their weight, but due to the nature of the young slugs, it was very difficult to remove them from the eggs at this weight and have recovery. Since the embryos would hatch and live after the eggs were dehydrated from 75 to 77.5 per cent of their weights, it is very probable that the young slugs lost considerably more than 40 per cent of their weight and still were able to recover.

CONCLUSIONS

There were several factors which influenced the time required to dehydrate to a definite weight: (1), the weight of the egg, (2), the humidity of the atmosphere, and (3), the age of the embryos in the eggs. Khalil found that four hours dehydration was not long enough to kill *Planorbis corneus* and that five hours was sufficient to kill every one of the young, even though they were in a jelly-like mass. We did not find that the time element was the important factor, since some of the young slugs were killed by four hours dehydration and others were not killed in seven hours. Apparently, Khalil never thought of noting the percentage of loss in weight of the *Planorbis corneus* eggs, but was only interested in the time required to kill the young.

The method of dehydration used in these experiments was quite rapid and dependable, the results being fairly constant in dry weather or in the rainy periods. The eggs of *Limax flavus* Linnaeus, which contained young embryos, hatched after they had lost from 80 to 85 per cent of their weight, while those eggs which contained full term embryos hatched after losing 70 to 75 per cent of their weight. Control experiments were performed which definitely showed that the young slugs lost weight during the dehydration treatment.

SUMMARY

1. The eggs of *Limax flavus* Linnaeus, which contained embryos, were dehydrated.

2. The eggs, which contained very young embryos, hatched, and the young lived after they had lost from 80 to 85 per cent of their weight.
3. The eggs, which contained full term embryos, hatched, and the young lived after the eggs had lost 70 to 75 per cent of their weight.
4. There were several factors which influenced the time required for the dehydration of the eggs: (1), the weight of the egg, (2), the humidity of the atmosphere, and (3), the age of the embryo.
5. The fully developed embryos could suffer a loss of 35 to 40 per cent of their weight and still survive.

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THE SUCCESSIONAL TREND AND ITS RELATION TO SECOND-GROWTH FORESTS IN SOUTHEASTERN ALASKA

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The forests of Southeastern Alaska are a northern extension of the Coast Forest Formation (Weaver and Clements, '29) varying, however, from this *Thuja-Tsuga* climax to become in the southern part a *Tsuga-Picea-Thuja* association, and north of latitude 56° approximately a *Tsuga-Picea* association. As the region is practically untouched by axe or saw, the climatic climax is undoubtedly the prevailing all-aged forest composed of *Tsuga heterophylla* 73 per cent, *Picea sitchensis* 23 per cent, *Thuja plicata* about 3 per cent, with occasional specimens of *Chamaecyparis nootkatensis*, *Abies lasiocarpa*, *Abies amabilis* and *Taxus brevifolia* making up the remainder. Approaching timber line *Tsuga heterophylla* often gives way to *Tsuga mertensiana* and *Chamaecyparis nootkatensis* is apt to be found in greater abundance.

Studies of reproduction, growth and timber yield have shown that the second-growth forests to follow the cutting of this climax will contain almost double the percentage of Sitka spruce existing in the old forest. It was found that volume of wood per acre varied with the amount of spruce in the young stands (Taylor, '29) and that this spruce content depended a great deal on seed bed conditions at the time of establishment. Pure stands of second-growth composed of either of the two species were low in yield; the best yields were obtained on areas containing about 75 per cent spruce by basal area.

In order to determine the best type of seed bed for Sitka spruce it was necessary to investigate various conditions of reproduction and growth, and in these studies successional trends were observed.

The region known as Southeastern Alaska extends in a northwesterly direction approximately from latitude 55° to 59° along the western edge of British Columbia, forming a belt of mountainous mainland and islands some 100 miles in width. It is characterized by an annual temperature of about 48° and an annual rainfall ranging from 80 inches at Juneau, near the northern end, to 160 inches at Ketchikan, near the southern end.

The dominant feature of the mainland and the central parts of the larger mountainous islands is the immense core of granite and diorite which occupies the central portion of the coast range throughout its length. Bordering the intrusive core is a band of closely folded metamorphosed strata in places having a width of several miles. At lower elevations, forming much of the more gentle slopes are found beds of stratified shales, sandstones, conglomerates and limestones, volcanic lavas and tuffs.

Dense forests extend from the water's edge to approximately 1500 feet elevation, varying in composition somewhat as timber line is reached. An attempt has been made to group some of the vegetation most characteristic of certain common habitats in an endeavor to indicate in general the preferences of these species:

Beach fringe.—*Pyrus diversifolia*, *Alnus oregona*, *A. sinuata*, *Salix* sp., and *Cornus stolonifera*.

Climax forest.—*Tsuga heterophylla*, *Picea sitchensis*, *Thuja plicata*, *Tsuga mertensiana* (Alpine), *Chamaecyparis nootkatensis*, *Vaccinium ovalifolium*, *V. parvifolium*, *Fatsia horrida*, *Sambucus pubens*, *Rubus spectabilis*, *Menziesia ferruginea*, *Cornus canadensis*, *Coptis asplenifolia*, *Lycopodium* sp., *Streptopus amplexifolius*, *S. curvipes*, *Moneses uniflora*, *Tiarella trifoliata*, *Rubus pedatus*, *Unifolium dilatatum*, *Lysichiton camtschatcense*, *Clintonia uniflora*, *Dryopteris dilatata*, *D. dryopteris*, *Polystichum munitum*, *Athyrium filix-foemina*, *Struthiopteris spicant*, *Pyrola uliginosa*, *Kruhsea streptopoides*, *Corallorrhiza mertensiana*, and *Ophrys cordata*.

Open stream banks and meadows.—*Rubus parviflorus*, *Urtica lyalli*, *Rubus spectabilis*, *Viburnum pauciflorum*, *Sambucus pubens*, *Rosa nutkana*, *Ribes bracteosum*, *Amelanchier florida*, *Epilobium angustifolium*, *Epilobium bongardii*, *Heracleum lanatum*, *Aruncus sylvester*, *Mimulus langsdorffii*, *Heuchera glabra*, *Fritillaria camschatcensis*, *Aquilegia formosa*, *Ranunculus bongardii*, *R. occidentalis*, *Geranium bicknellii*, *G. erianthum*, *Dodecatheon pauciflorum*, *Fragaria chiloensis*, *Saxifraga nelsoniana*, *S. nootkana*, *Sanguisorba sitchensis*, *Angelica genuflexa*, *Conioselinum gmelini*, *Ligusticum scoticum*, *Potentilla villosa*, *P. anserina*, *Viola langsdorffii*, *V. glabella*, *Nephrophyllidium cristigalli*, *Castilleja lutescens*, *Stellaria longipes*, *Claytonia sibirica*, *Actaea rubra*, *Aconitum delphinifolium*, *Lupinus arcticus*, and *Lathyrus maritimus*.

Muskegs.—*Tsuga heterophylla*, *Pinus contorta*, *Thuja plicata*, *Chamaecyparis nootkatensis*, *Ledum groenlandicum*, *Kalmia occidentalis*, *Empetrum nigrum*, *Andromeda polifolia*, *Vaccinium vitis-idaea*, *V. uliginosum*, *Menziesia ferruginea*, *Gaultheria shallon*, *Drosera intermedia*, *Eriophorum* sp., *Cornus canadensis*, *Trientalis arctica*, *Rubus chamaemorus*, *R. stellatus*, *Carex* sp., *Lysichiton camtschatcense*, *Sanguisorba microcephala*, *Argentina anserina*, *Unifolium dilatatum*, *Lycopodium* sp., *Pteridium aquilinum pubescens*, and *Caltha palustris*.

These are the groups found within the climax forest as a whole. The beach fringe varies from non-existent on rocky shores to a wide belt of brush on gently sloping beaches. Within the forest the species listed group themselves according to variations in habitat:—Skunk cabbage, *Lysichiton camtschatcense*, in the wet hollows, devil club, *Fatsia horrida*, elder, *Sambucus pubens*, and salmonberry, *Rubus spectabilis*, in the openings, especially on benches and flats, and ericaceous shrubs and herbs in stands having a large percentage of hemlock.

On the open banks of streams and in grassy meadows above high tide line the greatest variety of herbaceous plants is found. The muskegs or bogs of the region vary in size from an acre to several square miles and are interspersed throughout the forest. Transition zones are usually found about their edges in which the forest becomes scrubby, the forest floor swampy and ericaceous shrubs dense. Toward timber line where *Tsuga mertensiana* takes the place of *Tsuga heterophylla*, the vegetation takes on an alpine aspect.

The climax forest of the region is characteristically all-aged but when suddenly removed by windfall, storm, cutting or avalanche gives rise to an even-aged stand. The throw-back in the progress of successional stages is not sufficient, however, to give much information on the trend from bare soil to a climax. For this reason it was necessary to go to lands recently uncovered by glacial recession.

Cooper ('23) groups the vegetation of Glacier Bay, Alaska, into pioneer communities, willow-alder thickets, and conifer forests. He found the pioneer communities to be composed of a lichen, two mosses, nine willows, and the following:—*Epilobium latifolium*, *Dryas drummondii*, *Equisetum variegatum*, *Equisetum arvense*, *Poa alpina*, *Linnorchis* sp., *Saxifraga oppositifolia*, *Euphrasia mollis*, *Trisetum spicatum*, *Sagina saginoides*, *Pyrola secunda*, *Silene acaulis*, *Arctous alpina*, *Alnus tenuifolia*, *Lepargyreaea canadensis*, *Populus trichocarpa*, and *Picea sitchensis*.

In running a belt transect at Mendenhall Glacier, near Juneau, Alaska, the writer found that both *Picea sitchensis* and *Tsuga heterophylla* are present with the first pioneers but the latter for some reason dies out before many years, to reappear in the transition from sub-climax to climax. The transect was begun on glacial sand where the first sprinkling of pioneers was observed, 2170 feet from the face of the glacier. Figure 1 shows the pertinent information obtained.

It will be noted that at an age of 75 years and a distance of 6,070 feet from the face of the glacier a forest composed of 100 per cent of spruce is attained. This is the sub-climax forest. The forest floor is a thick mat of moss beneath which is found glacial sand and clay. Due to the accumulation of humus during the *Alnus-Salix-Populus* stage, good growth follows for some years, but with the closing of the coniferous crowns the hardwoods soon die, the debris becomes wholly coniferous and raw humus accumulates. Growth falls off as a result of this and also as a result of the roots penetrating the sterile glacial clay.

That these pure spruce stands are less productive than the usual type of young growth is shown by two half-acre plots taken in Glacier Bay by the writer. A comparison of these with normal second-growth of the same age and site index resulting from windfall in the climax forest is shown in table I. Figure 2 indicates the effect of spruce content on the site index.¹

¹ Site Index: The average total height of the dominant trees on a fully stocked sample plot at 100 years of age, obtained by reference to curves of total height over total age of trees.

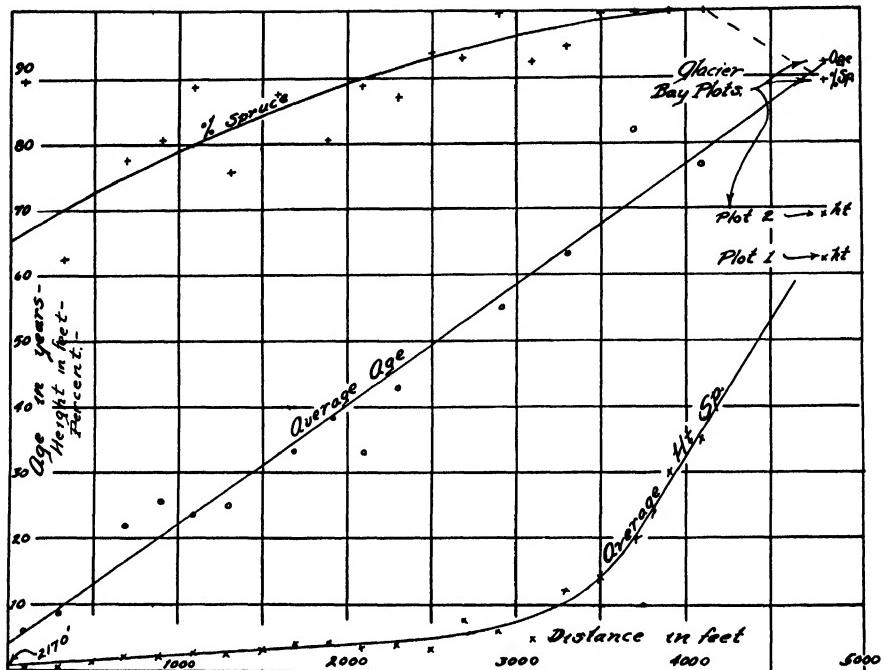


FIG. 1. The increase in age, height and percentage of spruce in composition, as related to increase in distance from the face of a glacier. Measurements were begun at 2170 feet from the face of the glacier, where vegetation started.

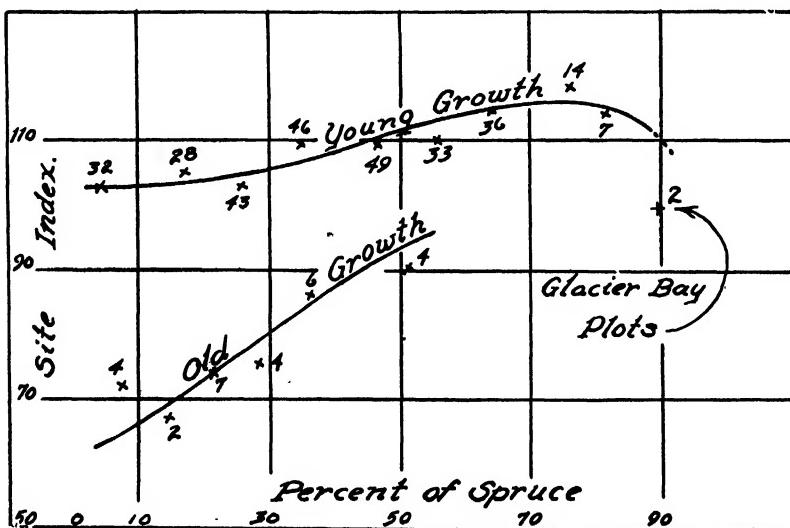


FIG. 2. The increase in site index (and consequently in yield) with an increase in percentage of spruce in the stand. The site index decreases when more than 75 per cent of spruce is found in the young stand.

TABLE I

Aver. Age Years	Site Index Feet	Trees per Acre Number	Basal Area per Acre Sq. feet	Aver. Diam. Inches	Merch. Vol. Stand 7" and over Cu. feet
Glacier Bay Plots. 92	102	552	228.99	8.7	5787
Average second- growth ¹ . . . 92	102	522	281.00	9.9	9090

¹ From yield tables for Southeastern Alaska.

The average height of the trees and the percentage of spruce on the two plots at Glacier Bay are entered on the chart (fig. 1) and indicate that such stands will not all reach the pure spruce stage by 75 or 80 years, but that the heights are not uncommon for such areas.

Pure stands of spruce, however, seem to be the sub-climax and are characterized in this instance by a sterile sandy soil covered by a mull composed of the debris of alder, willow and poplar. Open spacing and lack of organic material prevent fast height growth before the mull is formed and with the closing of the stand the hardwoods are lost giving rise to raw coniferous litter and duff and an increase in ericaceous plants within the forest. The more shade-enduring, less particular hemlock creeps in as an understory and with the falling of veteran spruce begins to take its place in the crown canopy and an uneven-aged forest composed of three-fourths hemlock is the stable result. This is shown by forests undisturbed by glaciation as well as by the type prevailing over the region.

The mull of hardwood leaves, however, is favorable to good spruce growth and the open glacial gravel and sand give rise to large numbers of spruce seedlings. Perhaps, then, any condition in the virgin forest which causes an exposure of mineral soil or fosters hardwoods or other vegetation characteristic of glacial land would also show a higher percentage of spruce. Data taken in various studies were reviewed and this was found to be correct in a large percentage of cases. It was also noted that a well-drained mineral soil is conducive to the growth of these hardwoods, especially alder, and that this combination, regardless of whether or not it occurred on glacial soil, gave rise to the largest percentage of spruce in mixture.

Avalanches in this region are common. They remove the old forest cover entirely and leave a path of mineral soil through the climax forest. The pioneers are a combination of plants typical of open mineral soils and large openings in the forest, such as: *Epilobium*, *Equisetum*, *Aruncus*, *Lycopodium*, *Empetrum nigrum*, *Vaccinium vitis-ideae*, *Alnus sinuata*, *Sambucus pubens*, and *Ribes bracteosum*.

The steeper, drier slopes are apt to have many lichens, and the vegetation is more apt to be characteristic of physiologically dry sites such as *Empetrum nigrum* and *Vaccinium vitis-ideae*. The lower, more gentle slopes with less

exposed rock and deeper soil are peopled at once with *Alnus*, *Sambucus*, *Ribes*, *Aruncus*, etc., and a gradual migration up the slope sets in until the alder brush covers the entire area. A summary of two such slides is shown in table II. At Neets Bay where the upper slopes are dry and lack much soil, the hemlock has germinated and persisted as a prostrate shrub making little or no growth. The lower slopes are covered by dense stands of young spruce with dying hemlock beneath. At Mud Bay the slide is older and covered by alder entirely.

TABLE II

	Neets Bay Slide Percent of species			Mud Bay Slide Percent of species		
	Picea	Tsuga	Thuja	Picea	Tsuga	Alnus
Gentle lower slope.....	57.0	37.5	5.5	40.8	15.0	44.2
Middle slope.....	10.3	88.0	1.7	29.8	24.6	45.6
Steep upper slope.....	11.8	85.6	2.6	7.48	76.4	16.12

The table is not entirely self-explanatory and might be somewhat misleading in that the hemlock on the lower slopes at Neets Bay is so oppressed that death is almost certain for a large percentage of it. At Mud Bay the upper slope hemlock is evidently the remnant of a stagnant seedling stand similar to that on the upper slopes of Neets Bay. The spruce average over 5 inches in diameter; the hemlock only two inches. Furthermore the alder mull soil and moderate shade are favorable to spruce germination and many tiny spruce seedlings, uncounted on the transect, are in evidence under the alder.

This seems to bear out the theory that a well drained mineral soil if not of too steep a slope is favorable to spruce, as first indicated by glaciated areas. The effect of slope itself is noted on all forested areas, for both the percentage of spruce and the site index increase with a decrease in slope (fig. 3). It is

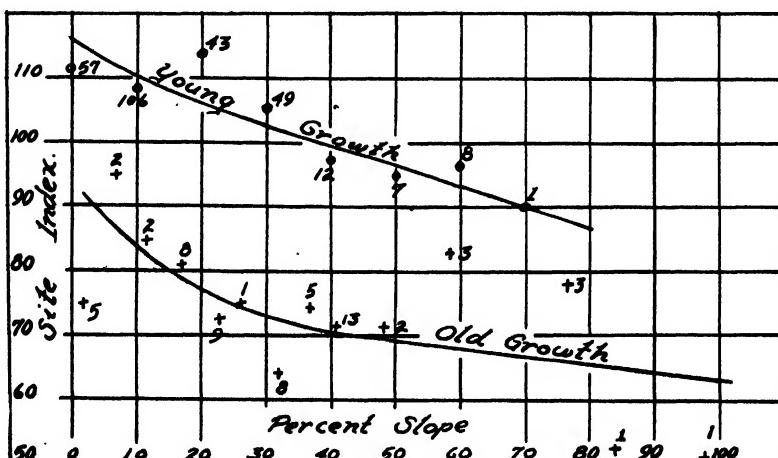


FIG. 3. Illustrating the decrease in site index as the slope becomes steep.

especially noticeable where limestone outcroppings occur at higher elevations and may be due to rapid leaching of food material from upper slopes and its accumulation on the gentle slopes and flats.

Although not mentioned by Cooper ('23) *Lupinus* sp. is common on many glacial moraines. The occurrence of this plant and the beach pea, *Lathyrus maritimus*, with good spruce reproduction has been noted. As the alders are known to fix nitrogen through the nodules commonly found on their roots, and as the two legumes are characteristic of nitrogenous soils, it may be suspected that the spruce finds available nitrates very favorable to early survival and growth. Munns ('22) noted such favorable action by lupine in the case of yellow pine, and Hesselman ('27) points out the superior growth of coniferous seedlings in easily nitrifying humus layers. The seepage of calcium carbonate from limestone would also favor more rapid decay, the formation of nitrate nitrogen and lower acidity (Perry, '28).

It seems then that the sub-climax is favored by a mineral soil for germination, a rapid accumulation of hardwood mull, or mild humus forming a type of soil similar to Tamm's "Brown Earth" ('30), and the presence of calcium to aid in decomposition.

Any factor in the climax forest favoring such a sub-climax should then favor a higher percentage of spruce in mixture, and it has been noted that this leads to higher site index and consequently to greater yields. Figure 2 shows the rise of site index as the percentage of spruce increases in the mixture for both young and old forests. A tendency for the curve to dip downward showing a decrease in site index as a pure stand is approached is noted.

It may be argued that estimating site by the use of plant indicators and soil conditions is not as accurate or as easy as judging the trees themselves, which is very true and their use for this purpose is not advocated. However, if good correlation is found between the vegetation and the percentage of spruce, and hence site index, it may be applied with advantage in judging the future site index on land already logged. It may serve as an indication of the condition of such land for producing good crops of spruce seedlings.

The common vegetation of the climax forest itself has been noted. It is entirely different from that found on recently glaciated lands and one might expect a gradual transition of vegetation types on lands progressing from open mineral soil devoid of organic matter to the raw acid humus of the climax. However, with the formation of the sub-climax spruce consociation all vegetation ceases to exist except the trees themselves, fast dying alder and cottonwood and a thick mat of moss. With the gradual opening up of the stand ericaceous vegetation develops.

In stands arising as a result of windthrow in the old forest or as a result of cutting by the Russians or Indians, or on abandoned village sites, are found examples of a close relation to a true sub-climax. Here the soil has an accumulation of litter from the climax forest mixed with mineral soil brought to the surface with upturned roots of windfalls or from dragging out logs. On

abandoned village sites trees have not grown for a long time and the raw humus has decayed. With the loss of acidity, the formation of organic food and plenty of light, plants typical of the open meadows appear, particularly *Epilobium* sp., *Urtica lyalli*, *Ribes bracteosum* and *Sambucus pubens*.

Such sites may be expected to be less favorable to spruce than the alder mull of slides or glaciated areas, but much more favorable than the raw humus of the virgin forest. However, they will vary in their degree of favorableness.

The vegetation on cutover land of the region is approximately that shown for open meadows with the exception that virgin forest types are present for several years, though usually declining in vigor. No data are available to show conclusively that any particular association of this intermediate vegetation is indicative of good growing conditions for spruce, and of those plants already mentioned, alder is characteristically along pole roads where dragging logs have exposed the soil and formed a water course, lupine is not extensive on logged off lands and the beach pea is, as its name implies, usually found close to the beach.

Rigg ('29) mentions the common stinging nettle, mountain elder, trembling aspen and wild gooseberry as indicators of good soil conditions. Wherry ('20) lists plants according to their acidity requirements, and the writer ('31) after seven year's observations in Alaskan forests has made a few slight alterations in the arrangement for local application. It will be noted that the minimacid group contains most of the plants common to open meadows and cutover areas, and the other two groups, most of those common in the forest.

Minimacid; pH 6.0-7.0.—*Alnus oregona*, *A. sinuata*, *Lathyrus maritimus*, *Ribes laxiflorum*, *R. bracteosum*, *Rubus spectabilis*, *R. parviflorus*, *Pyrus diversifolia*, *Epilobium angustifolium*, *E. latifolium*, *Sambucus pubens*, *Adiantum pedatum*, *Graminaceae*, *Montia sibirica*, *Fatsia horrida*.

Subacid; pH 5.0-6.0.—*Pteridium aquilinum pubescens*, *Athyrium cyclo-sorum*, *Dryopteris dilatata*, *D. dryopteris*, *Stellaria media* and spp., *Tiarella trifoliata*, *Gaultheria shallon*, *Menziesia ferruginea*.

Mediacid; pH 4.0-5.0.—*Vaccinium ovalifolium*, *V. parvifolium*, *Lysichiton camtschatcense*, *Streptopus curvipes*, *Unifolium dilatatum*, *Clintonia uniflora*, *Coptis asplenifolia*, *Rubus pedatus*.

Although it is known that nitrification will take place with the acidity as high as 2.9 pH and that the acidity itself is probably not the inhibiting factor where nitrification does not occur (Roniell and Heiberg '31) still there is a higher degree of nitrification in soils having more neutral reactions. Clarke ('24) notes a greater accumulation of ammonia in the acid soils than in less acid soils. Other conditions such as coldness and lack of aeration are often indicated by high acidity and therefore these groups are thought to indicate roughly soil conditions in the climax (mediacid) in the advanced stage of the sub-climax, just before the even-aged character of the stand is totally lost (subacid), and in the sub-climax soil type which regenerates to an advanced sub-climax as on cutover lands, abandoned villages and areas otherwise laid bare (minimacid)..

It is interesting to note that of the plants listed by Cooper as pioneers, seven are found in Wherry's list, as follows: *Epilobium angustifolium*, minimacid; *Salix* sp., circumneutral, (pH 6 to 8); *Alnus* sp., circumneutral; *Saxifraga* sp., circumneutral; *Pyrola* sp., subacid; *Silene* sp., minimacid; and *Populus* sp., circumneutral. Büsgen and Münch ('29) list as characteristic nitrophilous flora such plants as *Epilobium angustifolium*, *Ranunculus repens*, *Urtica dioica* and *Sambucus pubens*, among others.

The trend then is evidently from circumneutral *Alnus-Salix-Populus* mull, seemingly high in nitrate content and physically favorable for growth, through the minimacid salmonberry, thimbleberry, elderberry, currant stage characterized by slightly less favorable conditions, to the subacid and mediacid ericaceous shrubs, ferns and forest floor herbs. If these three groups may be properly differentiated on the basis of soil quality, growth and per cent of spruce, then perhaps any vegetation in the climax forest of the type commonly found in the minimacid sub-climax should indicate local conditions more favorable to spruce. Similarly on cutover land any vegetation of the circumneutral sub-climax should indicate the best conditions for spruce.

For the purpose of checking this theory, data from the virgin forest were examined. One hundred sixty-three plots taken over the region in the typical old growth were grouped according to site index. The per cent of each plant species on each site was then determined and charted as shown in figure 4. Although based on inadequate data for final conclusions, the chart shows a decrease in site quality with an increase in *Cornus* and *Vaccinium*, both of the mediacid type, and an increase in site quality with increases in *Rubus spectabilis* and *Fatsia horrida*, both of the minimacid type.

In order not to complicate the chart, only four species are shown. Ferns, mostly *Athyrium filix-foemina*, *Dryopteris dilatata*, and *D. dryopteris* showed trends similar to *Fatsia horrida* and *Rubus spectabilis*. *Lysichiton camtschatcense* and *Rubus pedatus* followed the trend of *Cornus canadensis*. Other species did not occur in sufficient quantity to be considered as dominant vegetation on the plots.

Applying this information to cutover areas, we may then expect to find a gradation of sites ranging from the poorest, as indicated by climax forest vegetation, to the best, as indicated by circumneutral vegetation. At the time of cutting, most areas, especially of pulpwood or piling, will have the mediacid type. By the time a stand of reproduction is thoroughly established it will have changed at least to the minimacid type and those tracts high in spruce content will tend toward the circumneutral. This type of change is noted by Ingram ('31) in the Douglas fir region and is probably due to the favorable effect on the raw humus of exposure to light as stressed by Hesselman ('26 and '27). It is probably one of the reasons spruce is apt to appear in largest numbers several years after cutting, except on the soils already more favorable to its reception.

Whether or not this information can be developed into any useful procedure in site classification on cutover land to be regenerated naturally is not known at the present time. Less complicated methods of site prediction will probably be used in the climax forests to be cut for pulpwood.

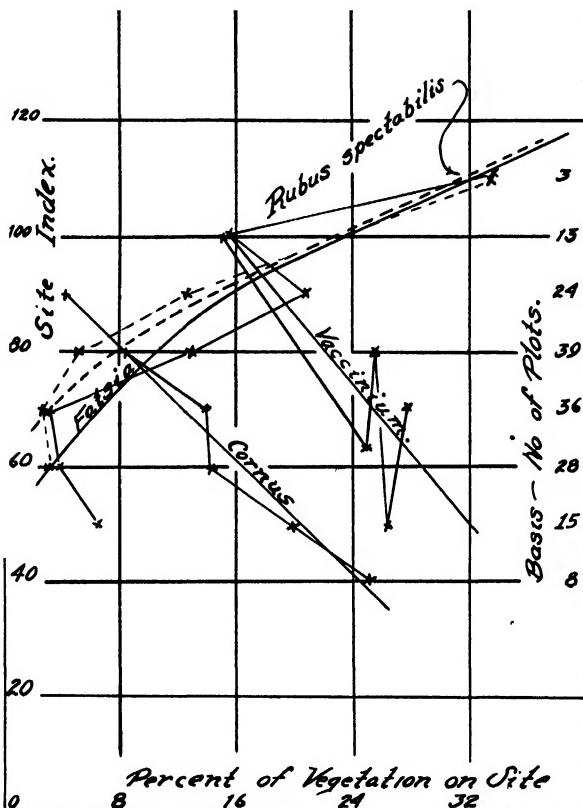


FIG. 4. The tendency of certain common species to vary in abundance with a change in site quality.

The investigation brings out, however, certain facts concerning favorable seed bed conditions for best spruce development and indicates the vegetation commonly associated with various soil conditions in the forest. It shows the trend of forest succession and related soil changes, and this information will all be of service in determining silvicultural methods which may improve soil condition and foster the increase of spruce in naturally regenerated stands.

SUMMARY

Successional trends were investigated in the climax forests of Southeastern Alaska. A list of characteristic plants occurring on four common habitats is given and compared with vegetation found on recently glaciated land. It is

shown that a pure spruce forest forms the subclimax in primary succession and that these stands are usually less productive than the subclimax which follows the removal of the climax in logging operations. This is evidently due to a proper mixture of the two principal species, spruce and hemlock, which fosters better growth of each. Soil conditions and vegetative growth on slides and other openings in the forest are compared and the common plants are grouped according to their soil acidity preferences.

It is shown that these groups of plants commonly occur on four different types of habitats and that each roughly indicates one of four stages in the successional trend.

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THE EFFECT OF FIRE ON THE PRAIRIE ANIMAL COMMUNITIES¹

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INTRODUCTION

The object of this study has been to ascertain the influence of spring burning upon the perennial and hibernating animal population of the sub-climax prairie. The Indians and early settlers burned the grasslands in the late fall or early spring believing that the early appearance of green grass would attract game or give an abundance of early feed for their domestic animals. However, Hensel ('23) of Kansas has shown that the grass is not more abundant on the burned than the unburned areas, but that the absence of dried grasses and other debris causes the burned areas to appear green earlier than the unburned areas. Other writers have shown that repeated burning of some prairie regions has prevented the invasion of forest into these regions.

Wheland ('27) found 54 species of insects belonging to eight orders, hibernating in *Andropogon scoparius* Michx. and *Andropogon furcatus* Muhl. Hayes ('27) says that if these grasses are burned many of the hibernating animals will be destroyed and those escaping will be affected by the increased evaporation and the lack of protection. Spring burning probably has less effect upon both the plant and the animal life than fall burning. Bouyoucos ('16) shows that the covering of mulch and vegetation acts as a blanket, which if removed in the fall destroys the homes of hibernating animals and allows much vegetation to be killed by frost.

LOCALITY

The area of study was the same as that used and described by Shackleford ('27). It consisted of strips of sub-climax prairie along the Illinois Central Railway one mile west of Seymour, Illinois. Another area along the railway one-half mile east of Bondville, was used for comparison.

Only the high prairie was considered, as the low prairie was too wet at the time of burning to be changed to any great degree. As mentioned before the high prairie covered with original sod was held in a sub-climax stage and included the following plants: wild parsnip (*Thaspium aureum* Nutt.), parsnip (near cultivated area) (*Pastinaca sativa* L.), prairie dock or rosin weed (*Silphium terebinthinaceum* Jacq.), compass plant (*S. laciniatum* L.).

¹ Contribution from the Zoological Laboratories, Univ. of Illinois No. 431.

red-seeded dandelion (*Taraxacum erythrospermum* Andr.), common dandelion (*T. officinale* Weber), sweet clover (*Melilotus alba* Desr.), ragweed (*Ambrosia bidentata* Michx.), ragweed (*A. artemisiifolia* L.), sunflower (*Helianthus* sp.), golden-rod (*Solidago* sp.), sedge (*Carex* sp.), Aster (*Aster ericoides* L.), bunch grass (*Panicum* sp.), blue grass (*Poa* sp.).

Many of the normal prairie dominants such as the common grasses, big blue stem *Andropogon furcatus* Muhl., and little blue stem *Andropogon scoparius* Michx., did not occur on this area except as occasional small groups of stalks. On roadsides where burning has not been practiced as much as along the railroad, these grasses are much more common and in a few places occur in small, dense, vigorous stands. Annual burning, following mowing, along a right of way (required by law), has caused these grasses to be replaced by the poas and weeds.

METHODS OF COLLECTING AND BURNING

The methods of collecting invertebrates were the same as used by Shackleford ('27). One m^2 of soil was examined carefully for animals present on the surface. Then one-tenth m^2 or about one square foot of soil was dug to a depth of three inches, brought into the laboratory, carefully examined dry, then placed in a fine meshed sieve and washed thoroughly in a pan of water.

Sweepings were made in the herb stratum when such a stratum was present. Fifty sweeps of the insect net were estimated as equivalent to the animals taken over one m^2 . The vertebrate fauna was listed by observation and cruising.

The methods just described are inadequate in the cold seasons. It is impossible to get the same species of animals in each collection during the hiemal and prevernal biotic season, due to the tendency of the animals to hibernate in aggregations in the most favorable spots. This is brought out in tables II and III. However, when several random samples were taken nearly all species were found in some of them.

However, the small random sample seems more accurate for the other seasonal socies because at that time many species have moved to the herb stratum and the total sample is increased by fifty sweeps of the sweep net. During the hiemal and prevernal biotic season there is no herb stratum and all data must be taken from the ground collections.

By an arrangement with the Illinois Central Railroad the area of study west of Seymour was not mowed nor burned from 1925 to 1928. But on March 10, 1928 it was set on fire by a locomotive. Most of the area, including some of the low prairie, was burned rapidly and clean. Stations were set aside for random sampling and observation during the spring and fall of 1928 and spring of 1929. Stations I and II were in the high prairie, *Lygus-Formica-Microtus* presocies of Shackleford. Station III was a high prairie station at Bondville which was kept unburned for comparison with I and II.

On March 14, 1929 Station II was burned over for the second time by appointment with the Illinois Central Railroad foreman. Station I was left unburned and used as a comparative station. A new Station IV was made by burning part of the Bondville Station III and was used as a comparison with Station III.

Weather instruments which consisted of a hygrothermograph and a soil thermograph installed in a weather shelter near Stations I and II, kept a continuous record of air and soil temperatures and humidity from September 18, 1927 to May 1, 1929.

OBSERVATIONS

The following observations on the animals and the vegetation were made immediately preceding and following each burning, March 10, 1928, and March 14, 1929. Only typical data are presented. The ground, at the time of burning each year, was quite damp; therefore the grass in many places was scarcely burned.

At the time of burning in 1928 the air temperature in the standard weather shelter rose, for approximately two hours, from 50° F. to 98° F. The humidity dropped from 85 per cent to 19 per cent. The soil temperature at a depth of 2 inches rose from 21° F. to 26° F. The soil temperature record showed such a slight increase of temperature at the time of burning that animals living beneath the surface would be little influenced by the heat. Upon examination, the surface showed: 10 charred spider cocoons per m²; remains of burned tenebrionid beetles, carabid beetles, and cut-worm larvae which were estimated as 3 each per m². The following living forms were found under a piece of wood, 3 by 8 inches, just after the fire had passed over the area: 19 chinch bugs, two cut-worm larvae, one ground beetle, one slug, two centipedes. The fire which had scorched and charred the surface of the wood was not hot enough to kill the forms beneath.

Animals such as *Aulax* larvae, living in the stems of *Silphium* and *Lactuca*, *Eurosta* and one or two species of lepidopterous larvae, living in golden rod stems, were killed when the fire burned the stems. The mortality in this was great, e.g., eight very small larvae were found in each of two golden rod stems in the unburned area.

The temperature of the soil for the earlier part of March was more constant on the unburned area than on the burned area. The ground under the vegetation on the unburned area was frozen until after March 23, 1929, while on the burned area it froze at night and thawed during the day. Bouyoucos ('16) shows that temperature on a barren area gets much lower at night and during cold days than on a soil covered by rubbish or vegetation. This condition caused the ground forms, such as earthworms, to come to the surface earlier on the burned area, as shown in table III.

April 2, 1929 a part of Station III at Bondville was burned and used as a comparison with the unburned portion of III. Observations were made of

the animal population in 1 m² of a burned and an unburned clump of bunch grass for a period of four weeks, April 3 to May 1. The animals were counted in the clump which measured 1/20 m² and calculated on the basis of 1 m² the results of which are given in table I.

TABLE I. Comparison of the numbers of animals in a bunch of burned bunch grass (*Panicum sp.*) with those in an unburned bunch of bunch grass (*Panicum sp.*)

Animals	Burned 1 m ²				Unburned 1 m ²			
	April 3	April 10	April 24	May 1	April 3	April 10	April 24	May 1
Rove Beetle (Aleocharinae).....	40	—	—	—	100	100	200	30
<i>Blissus leucopterus</i> Say (chinch bug).....	88	—	—	200	300	1600	600	20
<i>Stilbus apicalis</i> (Melsh) (Shining flower beetle).....	20	—	—	400	400	800	400	20
Spiders, 3 sp.....	20	—	—	60	120	120	120	10
Cutworm.....	20	—	—	20	40	40	40	10
Collembola.....	—	60	20	60	400	400	800	200
Ants.....	—	75	40	20	—	—	—	—
<i>Agriolimax campestris</i> Say (slug).....	—	—	—	—	240	220	240	—
Carabidae, 2 sp. (ground beetle).....	—	—	—	40	40	40	20	20
Elateridae, 2 sp. (click beetle).....	—	—	—	10	10	10	10	10
<i>Lygus kalmii</i> Stal. (plant bug).....	—	—	—	10	—	—	—	—
	188	135	60	820	1650	3330	2430	320

The first examination of the clumps was made on April 3, one day after burning. At this time the burned clump showed that a few of the animals survived the fire. These, however, were not found until a thorough search had been made beneath the charred litter in the center of the clump. The charred remains of 4 chinch bugs, 3 carabid beetles, and 1 cut-worm larvae were also found in the same bunch of grass.

On April 3 the animal life was very abundant in the unburned clump and little search had to be made. However, the unburned clump had much light debris made up of fallen and broken weed stems which made the animal life hard to find.

Table I shows that by April 10, the insects had left the burned clump and at the same time the number of animals had increased in the unburned clump. This change was noticed a week after burning and two days after a heavy rain which beat the debris and soil down well and left the burned area quite barren of litter, while in the unburned area there was much litter left for the protection of the animals. Evidently, the temperature at the time of the fire was not severe enough to kill all of the animals hibernating in the bases of the bunch grass, but as soon as the rains began, the remaining litter and soil became so packed that it left little protection to the animals and they probably migrated a distance of six feet to the better protected area. The high maximum temperatures after the burning was a factor influencing this migration.

TABLE II. List of animals collected during the prevernal period of 1928 over the burned and unburned Seymour Prairie with totals of animals found in each collection and each group of animals during the whole period

Animals	Burned area										Unburned area										
	Prevernal societies					Vernal societies					Prevernal societies					Vernal societies					
	1 m ²	3/12	3/24	4/14	4/29	5/7	5/12	5/24	Total	3/12	3/24	4/14	4/29	5/7	5/13	5/24	Total	3/12	3/24	4/14	4/29
Coleoptera, 16 sp.....	3	170	20	40	12	26	45	316	20	300	10	60	4	8	25	427	—	—	—	—	
Spiders, 14 sp.....	—	10	—	—	2	7	21	—	10	80	40	80	24	25	6	265	—	—	—	—	
Annelida, misc., 4 sp.....	—	200	10	—	—	20	10	240	—	60	—	—	—	—	3	63	—	—	—	—	
Cutworm larvae, 5 sp.....	10	20	10	20	—	10	10	80	14	—	20	50	21	50	20	175	—	—	—	—	
Ants, 4 sp.....	—	20	1500	750	100	—	110	2480	—	80	—	140	750	—	230	1200	—	—	—	—	
Hymenoptera, 6 sp.....	—	—	10	10	—	1	—	21	1	—	—	—	—	1	10	2	14	—	—	—	—
Tipulid larvae and adults	—	—	10	—	20	2	2	36	—	—	—	—	21	—	—	4	25	—	—	—	—
Hemiptera, 6 sp.....	10	—	70	140	10	10	10	250	—	—	—	—	70	—	—	6	76	—	—	—	—
Centipedes, 2 sp.....	—	20	—	—	—	—	—	—	20	—	—	—	70	—	—	10	—	—	2	82	—
Millipedes, 2 sp.....	—	20	—	—	—	—	—	20	—	—	—	—	—	—	—	—	—	—	—	50	50
Diptera, misc., 10 sp.....	—	—	10	—	—	6	—	7	23	2	—	—	—	1	—	19	8	—	—	—	130
Collembola, 4 sp.....	—	—	30	—	—	—	—	30	—	100	—	30	—	—	—	—	—	—	—	—	—
Orthoptera nymphs.....	—	—	—	—	—	3	2	5	10	—	—	—	—	—	—	—	—	—	4	4	—
Homoptera nymphs.....	—	—	—	—	—	17	10	20	47	—	—	—	—	—	—	—	—	1	7	8	—
Mites.....	—	—	—	—	2	2	—	—	4	—	—	—	1	—	—	—	—	—	—	—	1
Totals.....	23	470	1662	982	152	108	221	—	48	690	70	452	810	163	317	—	—	—	—	—	—
Grand total.....	—	—	—	—	—	—	—	—	—	3618	—	—	—	—	—	—	2550	—	—	—	—
Minus ants.....	—	—	—	—	—	—	—	—	—	2480	—	—	—	—	—	—	1200	—	—	—	—
Total minus ants.....	—	—	—	—	—	—	—	—	—	1138	—	—	—	—	—	—	1350	—	—	—	—

TABLE III. List of animals collected during the prevernal period of 1929 over the burned and unburned Seymour Prairie with totals of animals found in each collection and each group of animals during the whole period

Animals	Burned area					Unburned area					Prevernal species					Prevernal species				
	Prevernal species					Prevernal species														
1 m ²	3/4	3/16	3/23	4/3	4/13	4/17	4/24	5/1	Total	3/4	3/16	3/23	4/3	4/13	4/17	4/24	5/1	Total		
Coleoptera, 16 sp.....	—	30	45	20	8	20	10	10	143	50	10	43	5	4	40	10	10	172		
Mites, 4 sp.....	—	10	—	—	10	40	10	—	70	10	—	—	—	—	—	100	20	130		
Spiders, 14 sp.....	—	10	—	—	—	—	10	—	20	20	40	20	20	10	20	12	180	180		
Annelida, 4 sp.....	—	—	30	50	70	10	40	—	200	—	—	60	70	120	80	100	100	430		
Cutworm larvae, 5 sp.....	—	—	2	6	6	1	—	10	25	10	10	—	6	30	21	10	20	107		
Ants, misc., 4 sp.....	—	300	40	90	190	—	500	10	1130	—	—	10	40	3	200	10	500	500		
Hymenoptera, misc., 6 sp.....	—	—	—	—	—	4	7	2	5	18	—	—	—	4	7	20	5	46		
Hemiptera, misc., 6 sp.....	—	—	—	2	—	1	1	2	—	—	—	—	—	1	1	10	2	14		
Tipulid larvae, sp?.....	—	10	—	10	30	—	—	—	—	50	—	—	—	10	—	10	20	60		
Centipedes, 2 sp.....	—	—	4	10	—	—	—	—	—	14	—	—	—	20	10	20	10	60		
Millipedes, 2 sp.....	—	—	16	10	—	—	—	2	28	—	—	—	—	—	—	—	—	—		
Collembola, 4 sp.....	—	30	20	40	50	10	30	25	205	10	30	20	30	10	40	10	20	170		
Totals.....	—	390	169	236	369	89	604	62	—	100	90	123	191	152	469	300	709	—		
Grand total.....	—	—	—	—	—	—	—	—	1909	—	—	—	—	—	—	2134	—	—		
Minus ants.....	—	—	—	—	—	—	—	—	1130	—	—	—	—	—	—	763	—	—		
Total minus ants.....	—	—	—	—	—	—	—	—	779	—	—	—	—	—	—	1361	—	—		

By May 1 the animal life was well scattered but, since there was abundance of tender shoots on the burned area, many animals such as the flower beetles, *Stilbus apicalis* (Melsh) and chinch bugs, *Blissus leucopterus*, were attracted to this area.

EFFECT OF BURNING ON VEGETATION, SOIL ACIDITY AND ANIMALS

During April the vegetation on the burned area made a rapid growth while on the unburned area little growth was made until after May 1. This was true especially of *Panicum*, etc., but not true of all vegetation. The poas or blue grasses under close observation seem to grow equally well on the burned and the unburned area with this exception: blue grass that had been covered by litter was long and spindly while that on the burned plots was short and stubby and began to form seed heads at least a week ahead of that found on the unburned plot. However, this made little difference in the distribution of the insects as they were not active until after April 25, and table I shows that they were generally distributed at that time.

Further changes which took place after burning were as follows: violets, strawberry plants and seedlings of sweet clover and sunflower came in abundantly in places left bare by the removal of mulch. This shows that the heat of the fire was not great enough to destroy the seeds and the roots. Other plants were also increased in numbers and kinds, as shown by comparison of two quadrat counts made on the burned and unburned areas, May 1, 1929. All the changes in the vegetation influence the food and shelter of the animals in the vernal period.

The soil pH four weeks after burning was as follows:

Station III—burned pH 6.32.

Station IV—unburned pH 5.87, burned in 1928.

Station V—unburned pH 5.85, not burned in several years.

Any effect of a slight change in acidity upon the vegetation or animals is questionable.

Tables I, II and III cover the burned and unburned areas for the prevernal species for 1928 and 1929. It has been necessary, in making tables II and III, to group the animals by orders, families, or special groups, because of the irregular occurrence of the same species in consecutive collections, probably due to the small size of the sample. Upon checking over the species of invertebrates making up these small groups the number of species occurring on the burned area was considerably smaller during the early prevernal period than on the unburned area. During the late prevernal and early vernal period there was little if any difference in the number of species found on either area.

The number of animals occasionally was greater in the weekly collections on the burned than on the unburned area, because of the number of ants found in some of the collections. Since the ant nests are below ground and not seriously disturbed by fires, the number in any collection is determined

more by general conditions suitable for foraging than by actual numbers of ants within a small space. The total of animals other than ants was greater on the unburned area in both years.

The outstanding number of earthworms shown in the collection of March 24, 1928, was composed of individuals of one of the four species noted in table II, an unidentified small white species. These species were similarly affected by physical factors and accordingly are treated together. The variations of the earthworm population with variations in soil moisture are shown in table IV, based upon the number per m² to a depth of 8 cm.

TABLE IV

Date, 1929	Burned area		Unburned area	
	Per cent moisture	Number of earthworms	Per cent moisture	Number of earthworms
April 3.....	17.32	50	17.76	60
April 13.....	19.40	70	19.40	70
April 17.....	13.24	10	19.51	120
May 1.....	12.12	1	22.10	100

Other noticeable differences concerned both the invertebrates and vertebrates. Spiders were greatly reduced on the burned area. Two glass snakes, *Ophisaurus ventralis* (Linn.) were found in the high, dead grass near one of the pools in 1928. On April 13, 1929, a specimen was taken 150 feet from the pool in the grass that had not been burned. The white-footed prairie mouse, *Peromyscus maniculatus bairdii* (Hoy and Kennicot), or the prairie vole, *Microtus ochrogaster* (Wagner), had made burrows very abundantly over a strip of high prairie 5 by 40 feet at Station VI. These burrows were densely covered over with *Panicum* and *Poa*. When this area was burned over, the animals abandoned their burrows, went to an unburned area some hundred feet away, and made new runs and burrows under the dead grass. A rabbit that had a "form" in the grass and was seen quite often before the fire did not return afterwards.

Therefore, the whole nature of the community is considerably changed in both quality and quantity over the burned area during the early prevernal period, and probably to a slight degree later in the season. Repeated burning and cutting has modified the area by increasing the herbs and decreasing the grasses, so that it no longer represents a mature original subclimax prairie. It is rather an earlier successional stage presumably, so that it is similar to a developmental stage in which the grasses are just getting a foothold. This fact was not brought out by Shackleford ('29).

SUMMARY

1. One of the animal presocieties *Lygus-Formica-Microtus*, named by Shackleford, was found to be influenced by burning during the prevernal season, but showed little or no influence during the later vernal season or later.

2. The temperature in the soil at the time of burning of the Seymour Prairie, March 10, 1928, and March 8, 1929, was not great enough to kill all animals in hibernation.
3. The earthworm population was decreased appreciably by the evaporation due to the burning of the surface vegetation.
4. The population (exclusive of ants) decreased upon the burned area.
5. Comparison of a bunch of burned bunch grass with an unburned bunch showed that all animals not killed by burning migrated to nearby areas affording cover.
6. Some vertebrates moved to unburned areas because of lack of protecting vegetation.
7. Vegetation upon a burned area appeared earlier, grew more rapidly for a time, and seedlings of sweet clover, morning glory, sunflower and mint came in abundantly on all places left bare by fire.
8. Repeated burning produces a community in which herbs partially suppress grasses with probable corresponding changes in animals.

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REVIEWS

SOILS OF DANISH HEATH PLAINS¹

The work on the Danish heath plains is known to many who have come in contact with the problems presented by raw humus, podsolized soils and hardpan. In the effort to render these soils productive a good deal of interesting material has been secured on their physical and chemical properties, mostly through the investigations of Weis.² Weis's recent publication is a valuable addition to the information on these soils which he has already presented.

The present investigation has the advantage of having been made in a virgin heath plain, and therefore reveals the working of natural forces undisturbed by man. Although only a single locality is covered, that locality is typical of the podsolized heath soils of late glacial origin in Denmark and neighboring countries; and, since the results agree with those from earlier work, they are considered as having a general application.

The measurements of the average thickness of the horizons in 10 profiles is of interest in giving a conception of the kind of soil as illustrated by its profile. They are, in centimeters: A₁ raw humus, 8.9; A₁-A₂ Transition to bleached sand, 3.8; A₂ pure bleached sand (podsol), 7.0; A₃ humus hardpan (zone of accumulation), 7.4; B₁ iron hardpan (ortstein ?), 6.2; B₂ transition between iron hardpan and subsoil, 34.4; C subsoil begins at 67.8.

The dry weight of 1,000 cc. of natural soil in grams, is: raw humus 409.5, bleached sand 1,573.9, humus hardpan 1,243.3, and iron hardpan 1,405.6.

The pore space, which after total drying is filled with air, is generally taken up by the expansion of the hydrophile colloids, causing poor aeration. The percentage figures are, however, of interest: raw humus 81.4, bleached sand 39.0, humus hardpan 50.1, iron hardpan 45.1.

Important indications of the physical conditions are given by the hygroscopicity and the water holding capacity. The latter varied considerably in

¹ Weis, Fr. 1932. Fortsatte fysike og kemiske undersøgelser over Danske Hedejorder og andre Podsolanner. (Further investigations of Danish heath soils and other podsols.) (English Summary.) *Kgl. Danske Videnskabernes Selskab. Biologiske Meddelelser*, 10 (3): 1-202.

² Weis, Fr. 1921. *Forst. Forsogsv. Danmark*, 5: 343-352. *Biol. Abs.*, 10, entry 665, 1921.

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the raw humus, from 27.9 to 81.7 per cent, averaging 54.4. In the other layers the samples ran more uniformly, the averages being: bleached sand 7.1, human hardpan 22.1, iron hardpan 10.0, and subsoil 4.5. These figures show the sandy nature of the soil, and that its colloids are largely of organic origin.

The content of humus, or organic substances computed on a carbon percentage of 58, is: raw humus 27.0 (8.0-51.7); bleached sand 1.8; humus hardpan 12.7; iron hardpan 2.7; subsoil 0.2.

The soil contains a considerable quantity of nitrogen in the form of organic compounds bound up with the humus. The figures, in per cent, are: raw humus 0.49; bleached sand 0.03, humus hardpan 0.29, iron hardpan 0.06, subsoil 0.005. This represents a total of 22,500 kilograms of pure nitrogen per hectare, or approximately 18,000 pounds per acre, rather a large amount if it were in available form.

The carbon-nitrogen ratio shows great variation, between 18.8 and 37.9, but as a rule is between 20 and 30. In the organic matter of cultivated soils Waksman found a ratio of 10, varying between 8 and 12. Weis is investigating the hypothesis that a high C: N ratio means that the nitrogen is more easily converted to a readily assimilable form than with a low ratio.

As would be expected, the reaction is very acid, and, although becoming less so with depth, the subsoil is also rather strongly acid. The figures, in pH, are: raw humus 3.6; bleached sand 3.9; humus hardpan 4.1; iron hardpan 4.5; subsoil 4.8.

The latter part of the publication describes a sand drift area and the success of an experiment in cultivation of a green manurial crop for 2 years, followed by fertilization and tree planting in the third year. The buffer content here is so low that 5,000 kg. of calcium carbonate per hectare (about 4,000 pounds per acre) changed the reaction from pH 4.4-5.1 to 7.2-7.5. The trees have shown good growth. This treatment sounds rather intensive, but with good markets is no doubt worth the expenditure.

The factors which bring about the conditions investigated by Weis are but partially understood. The accumulation of raw humus is generally accepted as a climatic phenomenon; low temperature retards the activity of the micro-organisms which decompose the organic matter. Just what do we mean by low temperature? Certainly it is not the minimum reached in winter. Is it the sum of temperatures above an effective point? If so, what is the effective point for these particular soil microorganisms? Or do we come back to Merriam's⁸ basis of the mean temperature of the six hottest weeks in summer? Temperature is, however, not the only climatic factor in the development of raw humus and podsol. The amount and distribution of precipitation also play important parts.

⁸ Merriam, C. Hart. 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. *Natl. Geog. Mag.*, 6: 229-238.

There are other factors besides the climatic one. In a given climate we find raw humus in some places, and mull, with good decomposition, in others. It is evident that the character of the soil has a marked influence. In general, the indications point to the presence of lime in the soil as the factor responsible for the mull. Soil drainage also enters into the problem. In Sweden the reviewer has seen favorable soil conditions on areas of good drainage surrounded by raw humus where the drainage was poor. This is not a question of topography, for in Sweden and other northern countries poor drainage is common on slopes.

The vegetation must also be considered. Coniferous forests may cause the formation of raw humus in a climate and on a soil where mull is found under broadleaf trees.⁴

The factors above touched upon are but a few of those which, with our present limited knowledge, seem important. When they have been more thoroughly investigated will we be able to tell why *Calluna* dominates the heath plains, and what prevents the invasion of trees? Why, in a climate apparently suited to one formation does another persist? It would be particularly interesting to know why the conditions of the humus layers in the forests of northeastern United States are in general so favorable, and reproduction so good, in spite of abuse by the axe and fire. In his American visit in 1927, Hesselman remarked repeatedly on the favorable condition of our forest soils. Anyone familiar with European forests, their soil conditions and difficult natural regeneration, will understand what he means. The easy explanation, a new country with many more species, is hardly sufficient. Much more investigation is needed to answer this and other questions, and the results will be not only of great interest in themselves, but of much practical value.

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REGIONAL LIMNOLOGY¹

A number of papers dealing with the subject of regional limnology have been published during the past decade and the present brochure of Naumann discusses the problem in considerable detail. Regional limnology is defined as a comparative study of all known phases of our freshwaters, considering them not only as isolated individuals but also in relation to the natural conditions of the general region in which they are situated. The most important problem in such a study is the biological productivity of the water. This productivity is affected by a large number of ecological factors, of which

⁴ Fisher, R. T. 1928. Soil changes and silviculture on the Harvard Forest. *Ecology*, 9: 6-11.

¹ Naumann, Einar. 1932. Grundzüge der regionalen Limnologie. Bd. XI, Thienemann's *Die Binnengewässer*. xiv + 176 pp., 30 figs. Stuttgart.

temperature, light, and dissolved nutritive substances are of prime importance. Aquatic plants constitute the fundamental crop of biological material and the physical, chemical and biological factors which determine the size of this crop control the productivity of a body of water. The abundance of the animal population is dependent upon the crop of plants which serves, either directly or indirectly, as their source of food material.

The scarcity or abundance of the biological crop determines whether the water of a lake will have an abundance of dissolved oxygen at all depths during the summer period of stratification (oligotrophic type), or whether some of the lower water will be without free oxygen at this time (eutrophic type).

The author also discusses the effect of environmental changes produced by man on the productivity of lakes, such as pollution, and the general subject of aquiculture.

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ANIMAL ECOLOGY¹

Chapman's book on Animal Ecology is already well known because of the earlier mimeographed editions which date back to 1926. The value of the book has been increased by the revisions preceding its appearance in standard book form, which have allowed the inclusion of citations to more recent literature and the expansion of the bibliographies to include important papers previously omitted. It is a good book, well worth publication in its present standard form; and ecologists, particularly those interested in insects, or entomologists interested in the ecological aspects of their subject will undoubtedly appreciate the author's labors in making his survey of the subject more suitable for general use.

The materials available for treatment in a survey of ecology are many and varied. The present author has simplified his task by omitting, except incidentally, the biotic point of view. Plants appear largely as a part of the environment of animals rather than as associated organisms which together with the animals build up a biotic community. There is further simplification by the emphasis placed on insects. This emphasis is, however, uneven. The short section and bibliography on marine communities (pp. 252-260) mentions the practical absence of marine insects except the plague (sic) *Halobetes* (sic) and yet the material is presented from the point of view of marine ecology rather than discussing the influences of oceans upon terrestrial insect life. Of the treatment of *synecology*, 125 pages are devoted to aquatic aspects

¹ Chapman, R. N. 1931. Animal Ecology (with especial reference to insects) McGraw-Hill, 464 pp. The appendix gives a translation from the Italian of V. Volterra's Variations and Fluctuations of the Number of Individuals in Animal Species living Together. Pp. 409-448.

while only 33 pages deal with terrestrial animal communities in which insect components are much more important. Relatively little effort is made to evaluate the importance of insects as members of the various communities which are discussed.

The selection of material has been further influenced by an obvious predilection for relationships that can be illustrated by graphs or that have quantitative aspects which can be suggested or definitely measured. Thus the chapter on "biotic factors in autecology" deals entirely with the author's well-known work on "biotic potential" and "environmental resistance." Even the chapter on nutrition is made as quantitative as possible. The same concepts are emphasized in the synecological discussions. The tendency toward reducing ecological matters to a mathematical basis rather than leaving them as phases of natural history is commendable but there are many important aspects of ecology not yet capable of such treatment which deserve discussion in a book on ecology with special reference to insects. For example, social relations of insects are dismissed in a paragraph which includes reference to one of Professor Wheeler's books and to other scattered statements in the text.

As might be expected from a person with this point of view, autecology is emphasized, and even in the section on synecology, much attention is paid to the definitely measurable phases of the environment. The author quotes with apparent approval Shelford's 1929 statement that "Ecology is a science of communities" and then proceeds to devote half of his book to autecology which is defined as the equivalent of Adams' "individual ecology." This is a marked improvement over Shelford's own practice for, after his definition just quoted, he devoted practically the remainder of his book to various aspects of autecology.

In order to secure usable data to illustrate the discussion of quantitative aspects of relationships in animal communities, attention is limited to the relatively simple cases furnished by host-parasite and predator-prey relations. In this discussion some use is made of the material found in Volterra's statistical essay which is reprinted in English as an appendix. The author deserves praise for his enterprise in making this translation of one of Volterra's mathematical contributions available for American students; he himself makes relatively little use of the materials. Ecologists in general will be interested in Volterra's demonstration that, other conditions being equal, fluctuations in numbers of two species living together are periodic and the period depends solely upon the coefficients of increase and decrease and the initial conditions. This is a helpful suggestion for the study of rhythmic fluctuations in population numbers.

Volterra's mathematics are complicated as are those of Lotka, which are also cited; the reviewer and all others whose respect for such mathematics is greater than their facility in its use would be much more in Dr. Chapman's debt if the material had been more closely correlated with the complicated

population problems found in an ecological community. The reviewer suspects, however, that the difficulties inherent in this type of mathematics are sufficiently great to necessitate another and simpler type of mathematical attack upon these problems.

In other parts of the volume the reader has the feeling that despite revisions he is still dealing with lecture notes which have grown with the years as lecture notes will, rather than with carefully organized materials. The sections closely related to the author's own researches are definitely more coherent and more skillfully presented than are those based on compilations. In the latter there is relatively slight attention given to the growing concern with problems of community organization, and the use of such terms as "association" does not reflect the latest and most critical usage.

Elton has recently remarked on the great mass of data in ecology and on the shortage in general principles. A reader of the present book would be impressed similarly. Beyond the principles involved in "biotic potential" and in "succession" there is little stress on the use of principles even as a frame work upon which to hang the multitude of facts. Some ecologist should accept Elton's challenge and call attention to the ecological principles which are available for such use. They include in addition to those mentioned and among others such obvious ones as natural selection, environmental induction, toleration, co-operation, migration, isolation and adaptation, the last word not found in Chapman's index.

In conclusion, it has been the reviewer's experience that, of the ecological texts now available, graduate students turn by preference to the present book for reference study.

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NOTES AND COMMENT

A SIMPLE INSTRUMENT FOR RECORDING RAINFALL AND VELOCITY AND DIRECTION OF THE WIND

In the course of ecological studies of the pea aphid (*Illinoia pisi* Kalt.) it was observed that the infestation often dropped sharply after heavy rains. This was especially true when these rains were accompanied by winds of high velocity. A heavy rain, when driven by a strong wind, knocked many of the aphids to the ground. Some of them were able to regain the plants, but many were forced into the mud and killed by the beating rain. When collecting aphids in a net in order to obtain an infestation record, the writer observed that the number collected was greatly influenced by the wind velocity and temperature, both at the time of sweeping and for some time previously. As the available instruments for measuring and recording rainfall and velocity and direction of the wind were quite costly, necessitating a rather complicated set-up and requiring an electric current, he devised a comparatively simple but accurate instrument which records the three readings on one chart (fig. 1).

DESCRIPTION OF INSTRUMENT

This rain and wind recorder is equipped with a large eight-day laboratory clock movement and a $6\frac{1}{4}$ -inch aluminum drum. The drum is mounted on this clock and turned by it once in 24 hours. Very thin chart paper is used so that several thicknesses of it can be wound upon the drum without causing an appreciable error in time and the records need be changed only once a week. The charts are furnished in rolls each containing 90 feet. The entire roll is placed on the spindle and unwound by the clock, just enough friction being present in the spindle to keep a slight tension on the paper. Each week the chart is cut off and the blank end refastened to the drum by means of a special clip. As approximately 20 inches of chart are used every 24 hours, records that can be read with accuracy and unusual detail are obtained. This is an especially desirable feature when correlating wind velocity with time of rainfall. The chart spindle and the clock are mounted on a separate aluminum base and are removable, thus allowing the charts to be changed easily.

In designing this instrument, an attempt was made to make it as simple as possible, with few parts to get out of order. It is entirely mechanical in operation, requiring no electric current, and is therefore very convenient for field use.

The instrument is enclosed in a galvanized-iron case. One end opens as a door through which the clock is removed. The front of the case is equipped with a large glass, through which the operation of the instrument can be observed.

The three specific records which it was desired to secure with this machine were rainfall, wind velocity, and wind direction. The record of any one or all of these can be read for any 10-minute period during the 24 hours.

RECORDING THE RAINFALL

The rain is collected by means of a standard rain-gauge funnel. A small tube carries it to a siphon chamber containing a float.¹ The float rises as the chamber fills, and a fountain pen attached to the float makes a record on the chart. When the water reaches a set level, the siphon automatically starts to operate, thus emptying the chamber. The

¹ The float-siphon system of recording rainfall is a standard method in England. A gauge of this type is now built as the Fernley pattern under British patent 30,040 issued to Joseph Baxenbell in 1910.

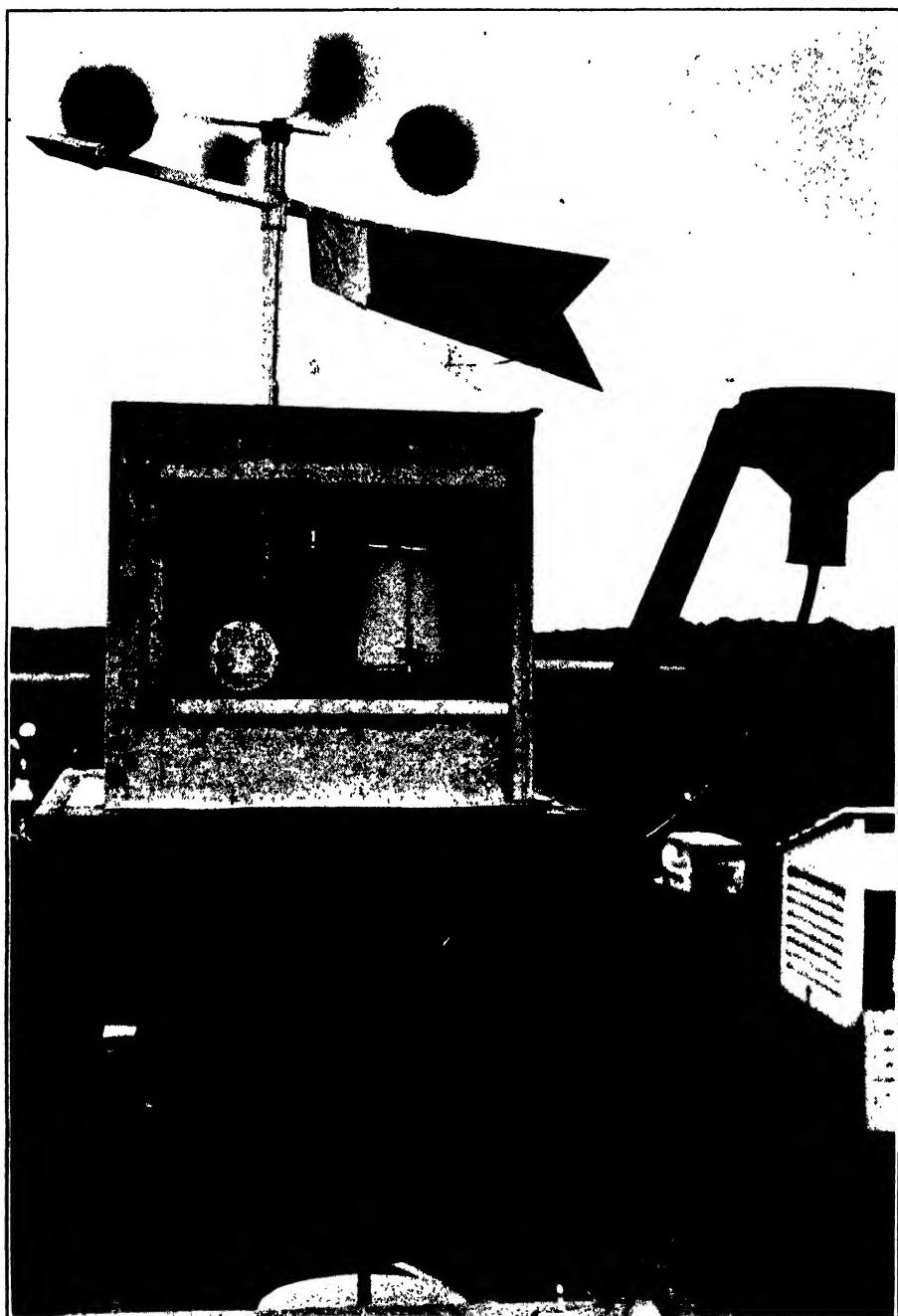


FIG. 1. Wind-rain recorder.

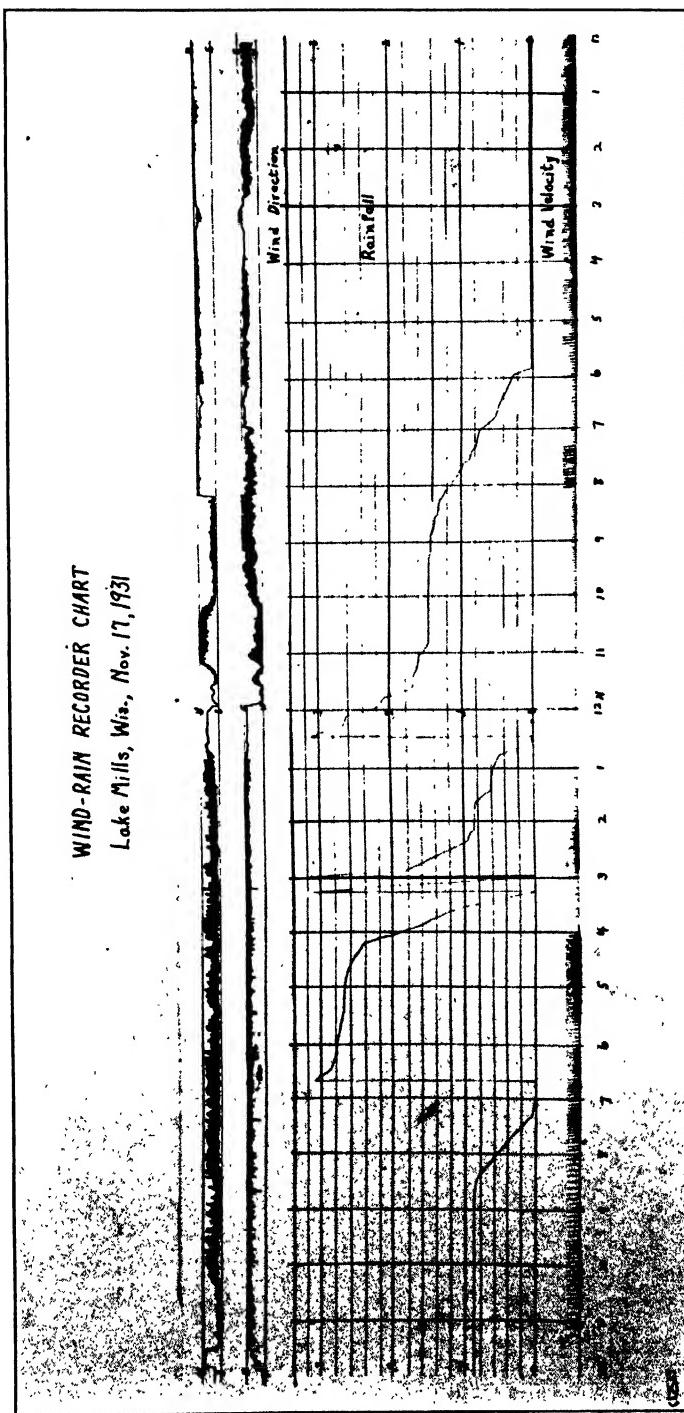


FIG. 2. Chart of rainfall and velocity and direction of the wind. The rain line from 6 to 9 A.M. indicates a light rain. The perpendicular line at 12:30 P.M. was made when the siphon chamber siphoned out. Note the very heavy rain from 3:00 to 3:20 P.M. Note also the shifting winds which blew from every direction.

ratio of the area of the funnel to the area of the siphon tube is such that it is possible to obtain an accurate record of as little as 1/100 inch of rain. It is also possible to record an unlimited amount of rainfall on the chart without attention to the instrument, since the siphon chamber is emptied each time it reaches the set level.

As the drum moves nearly 1 inch in an hour, the rainfall per unit of time can be determined with accuracy (fig. 2). If the 1 inch of rain fell in 30 minutes, a heavy rain is indicated.

On one or two occasions trouble was experienced in that the siphon became clogged with dirt, hairs, etc. To overcome this difficulty, a filter is being designed to clean the water before it reaches the chamber. Otherwise the machines have required very little attention.

In summary, the rainfall records give a complete picture of the total amount of rain, the amount falling in a given time, and the exact time of its beginning and ending.

RECORDING THE WIND VELOCITY

The wind velocity is measured with a standard cup anemometer. Each mile of wind is recorded on the chart by means of a pen actuated by a cam attached to the unit gear of the anemometer. The wind velocity can be read at the exact time of any rainfall. The velocity at this time gives a measure of the violence of the storm. It is also possible to adjust the instrument so that the wind velocity can be read in half-miles.

RECORDING THE DIRECTION OF THE WIND

The wind direction is obtained by means of two cams attached to a tube inside the anemometer shaft. This tube in turn is operated by an aluminum vane. Pens operated by the two cams record the wind direction on the chart. The upper pen shows a north wind when marking at its topmost position and a south wind when at its lowest position. When the upper needle is recording directly north or south, the lower needle is in a central position; conversely, when the lower needle is recording directly east or west, the upper needle is in a central position. This instrument also records northeast, northwest, southeast, and southwest. When the wind is from the northwest, the upper needle is between the central position and the north and the lower needle is between the central position and the west. The other directions have corresponding positions.

VALUE OF THE INSTRUMENT

One of these instruments² was constructed in the spring of 1930 and used during the entire season. It was so valuable that two more machines were made and used during the 1931 season, one at each substation.

The data obtained during the 1931 season have been very valuable in studies relating to ecology of the pea aphid. The records secured by such a machine, it is believed, would prove equally valuable to other problems both in entomological and related fields.

ABSTRACT

An instrument designed to measure rainfall, wind velocity, and wind direction simultaneously by means of a clock and a moving chart is described. This instrument has been used successfully in connection with a study of the effect of wind and rain on pea aphid infestations.

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² Although these instruments are not manufactured commercially, they can be secured by order. Information regarding them can be obtained from L. P. Haskins, 217 South Mills, Madison, Wis.

A NOTE IN REGARD TO CLASSIFICATION OF COMMUNITIES AND HABITATS

In his paper "Basic Principles of the Classification of Communities and Habitats and the Use of Terms" in the April issue of *Ecology* Dr. V. E. Shelford says "Consideration must, however, be had for the size of a community. The use of the same term for rocks moistened by dripping water and the whole abyssal bottom of the sea (Klugh, '23, pp. 371 and 373) is difficult of defense. The ocean floor, because of its great age, must be assumed to be a climax community, while rocks moistened with dripping water are local and usually unstable."

There are two quite distinct points which I wish to mention in regard to this statement. First, anyone reading the above paragraph, and not making reference to the original paper, *might* assume that I had used the same *name* for these two habitats, which would be ridiculous. A careful reading of the paragraph makes it clear that Dr. Shelford does not imply this, but that he means the use of the same term—presumably Association. In this, however, he is in error when he says the whole *abyssal* bottom of the sea, for reference to my paper will show that the case is, from his point of view, worse than he states, as I have placed the Abyssal as a systasis under the Benthic Association (the Sea-bottom) while I have given the Pladopetric (rocks moistened by dripping water) as an Association.

The second point is that I see no difficulty in defending the use of a term for any habitat, absolutely irrespective of size, provided the habitat is clearly marked off from all other habitats by its physical factors.

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